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THE DENTITION, SYSTEMATICS, AND PHYLOGENY OF *PSEUDOXYRHOPUS* AND RELATED GENERA FROM MADAGASCAR (SERPENTES: COLUBRIDAE), WITH DESCRIPTIONS OF A NEW SPECIES AND A NEW GENUS

JOHN E. CADLE¹

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ABSTRACT. *Pseudoxyrhopus oblectator* new species is described from Ranomafana National Park in southeastern Madagascar. This new species is characterized by having 21 midbody scale rows, a pale nape collar, and a dark brown or blackish dorsum with a narrow pale lateral stripe. It is most similar to *P. ambreensis* and *P. sokosoko*, but it differs from *P. ambreensis* in having eight supralabials with labials 4+5 touching the eye (seven with labials 3+4 touching the eye in *P. ambreensis*) and in details of the disposition of the pale lateral stripe. *Pseudoxyrhopus oblectator* differs from *P. sokosoko* in having a pale nape collar (absent in *P. sokosoko*).

Hemipenial and dental characters of *Pseudoxyrhopus* are reviewed, and some previous observations are corrected. Based on the new observations, relationships and previously erected species groups within *Pseudoxyrhopus* are reassessed. Hemipenes of

Pseudoxyrhopus are bilobed and are entirely spinose, with controlineal sulci spermatici. Contrary to previous reports of a single maxillary fang in three species, all species of *Pseudoxyrhopus* have a pair of enlarged posterior maxillary fangs and some species and individuals lack a maxillary diastema.

The dentitions of *Pararhadinaea melanogaster*, *P. albignaci*, and *Heteroliodon occipitalis* are re-described. Based primarily on substantive dental differences from *P. melanogaster*, *Exallodontophis* new genus is created to accommodate "*Pararhadinaea*" *albignaci* Domergue. *Exallodontophis* is characterized by an unusual maxillary dentition consisting of a pair of considerably enlarged teeth in the middle of the maxilla, followed by an exceptionally broad diastema and a pair of fangs. This arrangement is unlike that of any other Malagasy snake. Some dental characters previously attributed to *Pararhadinaea* were based on *Exallodontophis*. Although the dentition of *Pararhadinaea melanogaster* Boettger (type species of *Pararhadinaea*) is unusual in some respects, its maxillary and dentary dentition are unlike those of *Exallodontophis*. Present evidence suggests that *Exallodontophis* is more closely related to *Pseudoxyrhopus* than to *Pararhadinaea melanogaster*.

Several characters of the dentition provide synapomorphies suggesting relationships among *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, *Pararhadinaea*, and other Malagasy colubrids. Hinged teeth are reported for the first time in all four genera, and this derived character is shared with *Liophidium*. *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* share, in addition, enlarged median dentary teeth, and in the former two genera these enlarged teeth are followed by a diastema. The dentary dentition of *Pararhadinaea melanogaster* is unique in having five or six greatly enlarged and widely spaced posterior teeth. The teeth in *Heteroliodon* and *P. melanogaster* are unusual in having blunt, anteroposteriorly compressed tips similar to teeth in species of *Liophidium*. Several unusual features of the dentition of *Pseudoxyrhopus*, *Heteroliodon*, *Exallodontophis*, and *Pararhadinaea*, including hinged teeth, enlarged median dentary teeth and diastema, and enlarged median maxillary teeth and broad diastema, are probably related to diets rich in skinks and/or gerrhosaurids. Known diets of *Pseudoxyrhopus* species include skinks, skink eggs, and rodents.

Hinged teeth and a modified pattern of tooth replacement support the relationship of *Liophidium* to *Pseudoxyrhopus*, *Heteroliodon*, *Exallodontophis*, and *Pararhadinaea*, in contrast to a recent hypothesis that the last four genera had no close Malagasy relatives. Consequently, the *Pseudoxyrhopus* group comprises five genera: *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, *Pararhadinaea*, and *Liophidium*. A phylogenetic analysis of the *Pseudoxyrhopus* group based on morphological characters resulted in three equally parsimonious trees that differed in their placement of *Pararhadinaea*. One of the most parsimonious trees (MPTs) and the strict consensus of the three trees

had the same topology: (((*Pseudoxyrhopus*, *Exallodontophis*), *Heteroliodon*), *Pararhadinaea*, *Liophidium*). In the other MPTs *Pararhadinaea* was the sister group to either *Liophidium* or to *Pseudoxyrhopus*-*Exallodontophis*-*Heteroliodon*. Some characters of the dentition in the *Pseudoxyrhopus* group are shared with mainland African species of *Lycophidion*, *Chamaelycis*, *Mchelya*, and putatively related genera (Group II of Bogert). However, other substantive differences between the African and Malagasy groups in dentition and hemipenial morphology suggest that the shared similarities in dentition may be convergences related to diet. Moreover, differences in the morphology of the hemipenes and dentition among some of the Group II genera suggest that additional investigation of the monophyly of this group is warranted.

INTRODUCTION

The Malagasy colubrid genus *Pseudoxyrhopus* includes 10 species of apparently relatively secretive snakes (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). Six of the 10 species were described in the last century, but the other four have been described since 1993. Most species are known from relatively few specimens. During a survey of the herpetofauna of Ranomafana National Park (see Cadle, 1995, 1996a,b) an apparently new species of *Pseudoxyrhopus* was obtained and is described herein. The new species conforms to diagnoses of the genus *Pseudoxyrhopus* (Boulenger, 1893; Raxworthy and Nussbaum, 1994) in having a median series of enlarged dentary teeth, and it is phenetically very similar to several other species in the genus. However, no diastema precedes the posterior maxillary fangs, in contrast to the condition previously reported for other species of *Pseudoxyrhopus*.

In describing the new *Pseudoxyrhopus* I discovered two previously unreported dental characters for the genus (hinged teeth, dentary diastema). Moreover, existing descriptions of dentition in *Pseudoxyrhopus* and its presumed close relatives, *Heteroliodon* and *Pararhadinaea*, were incomplete and inaccurate to varying degrees. Thus, I provide here an extended discussion of these characters and correct errors in previous literature. The revised

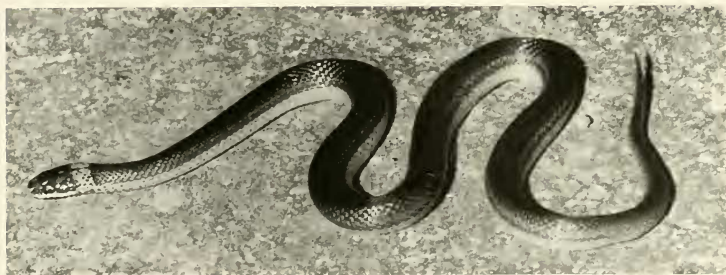


Figure 1. Holotype of *Pseudoxyrhopus oblectator* (MCZ 182292) new species, in life. Approximately $\times 0.7$.

morphic (01), or uncertain (?). Both ACCTRAN and DELTRAN character optimizations (accelerated and delayed transformation, respectively) were employed. An explicit outgroup for rooting purposes was not available for the study group. Trees were rooted using an artificial ancestor whose states for some characters were inferred when the ancestral state for the ingroup (the *Pseudoxyrhopus* group) seemed clear based on consideration of likely outgroups. Other characters in the ancestor were coded as uncertain (?) when the ancestral state of the ingroup could not be reliably inferred. The argumentation for each character state in the hypothesized ancestor is provided in the character discussions; alternative codings for some terminal taxa were used for several characters. Alternative trees were evaluated in terms of overall length (total number of steps) and two measures of correspondence between data and the trees: the consistency index (CI), which was calcu-

lated after excluding uninformative characters, and the retention index (RI). Trees of minimal length (most parsimonious trees [MPTs]) were considered the best estimates of phylogenetic relationships. Explicit alternative phylogenetic hypotheses were tested by using a constraint tree that maintained the monophyly of a particular group of interest while allowing all other ingroup taxa to vary in position. The lengths of MPTs obtained with and without constraint were compared.

DESCRIPTION OF A NEW SPECIES OF *PSEUDOXYRHOPUS*

Pseudoxyrhopus oblectator new species

Figures 1, 2, 4, 5, 17

Holotype (Figs. 1, 2, 17). MCZ 182292 (field number JEC 14923), an adult male collected 10 January 1998 from Mahajo Stream (a southern tributary of the Ranomena River), Ranomafana National Park (northern sector), Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar; 1,110 m elevation [approximately 21°13'S, 47°28'E]. John E. Cadle, Talata Pierre, and Rajeriarison Emile, collectors.

Paratype. MCZ 181287 (JEC 11467), a juvenile male collected 27 December 1991 by J. E. Cadle from a pitfall trapline at Talataky, Ranomafana National Park, Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar, 950 m elevation [21°15'50"S, 47°25'10"E].



Figure 2. Head and anterior body of *Pseudoxyrhopus oblectator* (MCZ 182292; holotype) new species, in life. Approximately $\times 1.25$.

Referred Specimen. MCZ 180299 (JEC 12722), an adult male collected 15 February 1993 by Dan Turk at Ambodiamontana (6 km W Ranomafana at entrance to Ranomafana National Park), Fivondronana Ifanadiana, Fianarantsoa Province, Madagascar, 910 m elevation [21°15'20"S, 47°25'18"E]. MCZ 180299 is a badly damaged roadkill and is somewhat desiccated, but all scale counts were determinable. The damaged skull of this specimen was removed for osteological examination. No specimens are known aside from the types and referred specimen.

Distribution (Fig. 3). Known from 900–1,100 m elevation near the type locality. The three known localities are within 10 km (airline) of one another within the Ranomafana National Park.

Etymology. The specific epithet, *oblectator*, is a masculine Latin noun in apposition meaning charmer, delighter, or pleaser. Most species of *Pseudoxyrhopus* are infrequently encountered and the epithet refers to the delight these uncommon snakes bring when they are found.

Diagnosis. *Pseudoxyrhopus oblectator* is characterized by having a pale nape collar in juveniles and adults, 21 midbody scale rows, fewer than 160 ventrals (known range, 143–158), fewer than 50 subcaudals (known range, 44–48), all subcaudals paired, and eight supralabials (4+5 contacting the eye). Coloration is dark brownish black middorsally, a pale lateral stripe on scale rows 4+5 at midbody (involving other rows elsewhere), and pale coloration on the lower three dorsal scale rows. Because few specimens (and no females) are known, ventral and subcaudal counts may be expected to vary somewhat from these values.

No species of other genera in the *Pseudoxyrhopus* group have 21 scale rows. Five other species of *Pseudoxyrhopus* have 21 midbody scale rows: *P. ambreensis*, *P. analabe*, *P. heterurus*, *P. quinquelineatus*, and *P. sokosoko* (Nussbaum et al., 1998). *Pseudoxyrhopus analabe* differs from *P. oblectator* in having all subcaudal scales undi-

vided (entire). In *P. heterurus* the anterior subcaudals are undivided and the posterior ones are divided. *Pseudoxyrhopus quinquelineatus* differs from *P. oblectator* in having a rather pointed snout and countersunk lower jaw (rounded snout and normal lower jaw in *P. oblectator*) and a pale brown or yellowish dorsum with five narrow dark lines (blackish brown without dark lines in *P. oblectator*). *Pseudoxyrhopus oblectator* is most similar to *P. ambreensis* and *P. sokosoko*. All three species have 19–21 dorsal rows and the posterior reduction occurs by loss of row 5.

Pseudoxyrhopus oblectator and *P. ambreensis* are similar in having a pale nape collar, similar scale counts, a light lateral line on a dark dorsum, and pale lower dorsal scales. The two most distinct differences between these species are the number of supralabial scales (eight with 4+5 touching the eye in *P. oblectator*; seven with 3+4 touching the eye in *P. ambreensis*) and the disposition of the pale lateral stripe. In both species the pale stripe is less distinct anteriorly than posteriorly (Raxworthy and Nussbaum [1994] stated that the stripe began at midbody in *P. ambreensis*, but the stripe was evident all the way to the neck in preserved specimens I examined under magnification). In *P. oblectator* the stripe occupies dorsal row 5 the length of the body. Anteriorly it is more or less restricted to row 5, broadening to include the upper half of row 4 at the point where the dorsal count increases to 21 and broadening again toward the posterior end of the body to include the lower half of row 6. In *P. ambreensis* the lateral stripe occupies row 5 anteriorly, row 6 at midbody, and row 5 posteriorly; except for irregular involvement of parts of rows 4 and 6 posteriorly, the stripe in *P. ambreensis* is usually less than one scale row wide (reduced to series of dashes anteriorly). Thus, the lateral stripe is broader in *P. oblectator* than in *P. ambreensis*. In *P. oblectator* the stripe continues onto the tail, where it broadens to occupy virtually the entire lateral surface (Fig. 1); in *P. am-*

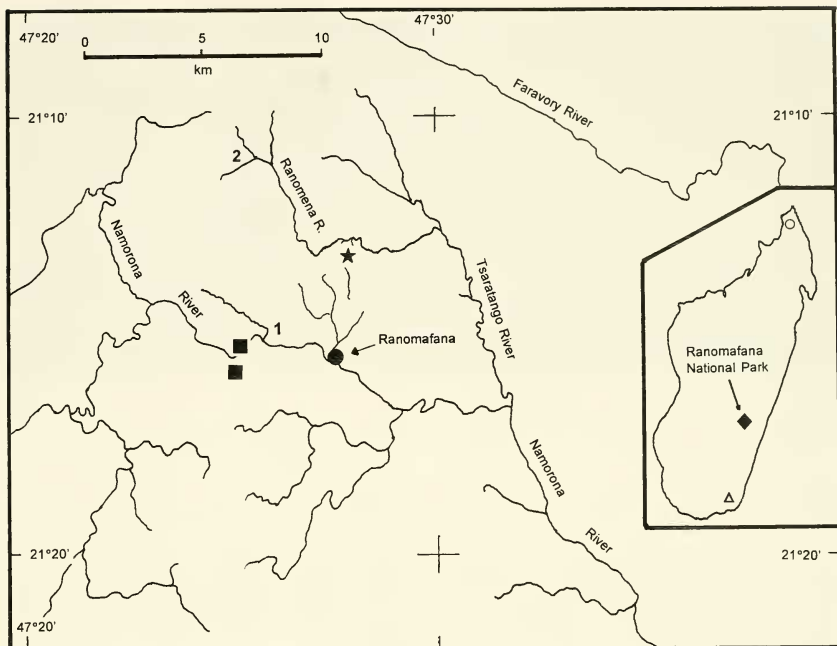


Figure 3. Distribution of *Pseudoxyrhopus oblectator*. Map detail is the central portion of Ranomafana National Park and vicinity. ★ = type locality of *P. oblectator*; ■ = other known localities for *P. oblectator*; ● = town of Ranomafana. Localities mentioned in the text: 1 = the village of Ambatolahy; and 2 = the approximate western edge of the Ranomana River swamps. Inset: Location of Ranomafana National Park and the distributions of *P. ambreensis* (○) and *P. sokosoko* (△); for these species symbols represent multiple contiguous localities (see Raxworthy and Nussbaum, 1994, for specific localities).

breensis the lateral stripe ends at the level of the vent (see Fig. 13; Raxworthy and Nussbaum, 1994; personal observations).

Several other more subtle features potentially distinguish *Pseudoxyrhopus oblectator* and *P. ambreensis*. The color of the nape collar is described as pale brown in life in *P. ambreensis* (Raxworthy and Nussbaum, 1994), whereas it was pale orange in the adult specimens of *P. oblectator*. However, too few specimens are accompanied by coloration data to be sure that this difference is consistent. *Pseudoxyrhopus oblectator* also has a slightly larger eye than *P. ambreensis* (0.30–0.34 times head depth versus 0.20–0.25 times head depth),

but these measurements are rough guides only because head measurements lack precision. The difference is readily apparent by comparison of specimens side by side.

Pseudoxyrhopus sokosoko lacks a pale nuchal collar, whereas a collar is present in *P. oblectator*. *Pseudoxyrhopus oblectator* and *P. sokosoko* are very similar in scale counts and the position of the pale lateral stripe. In the type specimen of *P. sokosoko* (fide Raxworthy and Nussbaum, 1994) and in UMMZ 203660 the stripe is on scale rows 4+5 posteriorly but is not evident anteriorly. In two other specimens (UMMZ 203661, 209689) the stripe is evident under magnification from the neck to the tail

TABLE 1. SCALE COUNTS, MEASUREMENTS, AND OTHER DATA FOR THREE SPECIMENS OF *PSEUDOXYPHOPUS OBLECTATOR*. BILATERAL COUNTS (E.G., HEAD SCALES AND POSTERIOR SCALE REDUCTION) ARE GIVEN FIRST FOR THE LEFT SIDE, THEN FOR THE RIGHT.

	MCZ 182292 (holotype) ¹	MCZ 180299	MCZ 181287
Sex	male	male	male
Total length (SVL ¹) (mm)	392 (325)	407 (329)	178 (143)
Tail length (mm)	67	78	35
Tail length/total length	0.17	0.19	0.20
Maxillary teeth	14+2	17+2	16+2
Dorsal scales	19-21-19	19-21-19	19-21-19
Ventral scales	158	146	143
Subcaudal scales	44	47	48
Posterior scale reduction	-5(93)	-5(100)	-5(73)
	-5(94)	-5(100)	-5(74)
Anal scale	divided	divided	divided
Preocular scales	1, 1	1, 1	1, 1
Postocular scales	2, 2	2, 2	2, 2
Temporal scales			
Anterior	1, 1	1, 1	1, 1
Posterior	2, 2	2, 2	2, 2
Supralabial scales (touching eye)	S, S (4+5)	S, S (4+5)	S, S (4+5)
Infralabial scales	9, 9	9, ?	9, 9

¹ SVL = snout-vent length.

and has a slightly different distribution from that of *P. oblectator*: anteriorly on scale row 5, rows 5 and 6 at midbody (rows 4 and 5 in *P. oblectator*), and posteriorly broadening to include row 5 and adjacent portions of rows 4 and 6 as in *P. oblectator*.

Data on the Holotype. The holotype is a well-preserved male with everted hemipenes (the left one removed for illustration) whose identifying characteristics are given in Table 1. The specimen is probably an adult, as indicated by somewhat convoluted vasa deferentia and mineralized hemipenial spines (for discussion, see Cadle, 1996b: 43-44).

Description. Meristic data and measurements for the three known specimens are reported in Table 1. The following description is based on all three specimens except that measurements of eye and head proportions for MCZ 180299 were not included (head damaged). Largest specimen MCZ 180299 (male, 329 mm snout-vent length [SVL]). No female available. Tail relatively short, 17-20% of total length. Dorsal scales smooth, lacking apical pits,

and in 19-21-19 rows. Posterior reduction by loss of row 5. Ventrals 143-158, anal plate divided, subcaudals 44-48 and all paired.

Rostral scale slightly visible from above, 1.5-1.8 times wider than high. Paired internasals wider than long, each about half the size of a prefrontal. Paired prefrontals wider than long. Frontal roughly hexagonal in the adults (anterior angle very obtuse) but pentagonal in the juvenile. Frontal 1.2-1.6 times the length of the interparietal suture and 1.3-1.4 times longer than the distance from its anterior edge to the tip of the snout. Each parietal about 1.5 times longer than broad. Nasal divided posterior to nostril by a ventral suture and a shorter dorsal suture. Loreal small, squarish. One preocular, two postoculars; temporal series 1+2. Supralabials eight, with 4+5 touching the eye. Infralabials nine, the first pair in contact behind the mental; the first four infralabials broadly in contact with the anterior genials and the fifth infralabial contacting them narrowly or at a point. Anterior genials slightly long-



Figure 4. Maxillary dentition of *Pseudoxyrhopus oblectator* new species (MCZ 180299). Digital photograph of the posterior end of the right maxilla showing lack of a diastema in this species. Teeth are detached anterobasally, a manifestation of the fibrous hinge attaching the teeth on their posterior edges (see text). The posterior fang is missing from this specimen; its socket is in the lunate space posterodorsal to the anterior fang. Scale bar = 1 mm.

er than posterior genials; only the fifth infralabial contacts the posterior genials. No scale organs or pits visible on head scales.

Overall body form slender but robust. Head slightly wider than neck. Ventrolateral edge of body rounded. Pupil round. Eye small, about 0.3 times head depth at the middle of the orbit in adults, about 0.1 times head length (tip of snout to tip of retroarticular process), and about 0.85 times the distance from its anterior edge to the posterior edge of the nostril.

A pale nape collar in juveniles and adults (white in the juvenile, orange in the adults). Dorsum dark brown to black with a pale lateral stripe (on dorsal scale rows 4+5 at midbody) from the neck to the tip of the tail and pale lower dorsal rows. Venter light colored with fine dark stippling.

Dentition (Fig. 4). Maxillary teeth 14-17+2, the rear fangs greatly enlarged and ungrooved; posterior fang slightly offset laterad. No diastema between the fangs and the more anterior teeth. Fangs strongly compressed (anterior edge broader than posterior) and with a knifelike posterior edge. Additional tooth counts from the prepared skull of MCZ 180299: palatine teeth 13-12; pterygoid teeth 21-21; den-

tary teeth 17 on the right (left dentary broken). Maxillary teeth except for the fangs and dentary teeth except for the enlarged median series are hinged in the sense of Savitzky (1981).

The first six dentary teeth of MCZ 180299 gradually increase in size; teeth 7-9 are noticeably enlarged, followed by an abrupt transition to smaller teeth 10-17. Dentary formula 6(7-9)-8 = 17. No diastema in the dentary tooth row of MCZ 180299, but a dentary diastema large enough to accommodate about a single tooth is present in the holotype. On the right side of the holotype five small dentary teeth are followed by three greatly enlarged teeth (posterior dentary teeth not investigated). Anterior and posterior dentary teeth subequal.

Hemipenis (*Fully Everted Left Organ of Holotype*; Fig. 5). Deeply bilobed, noncapitate, entirely spinose (acalculcate). Sulcus spermaticus bifurcating just below the lobes and with centrolateral branches. Total length of everted organ 9.5 mm, bilobed for the distal 5.5 mm (58%). In overall form the organ has a slightly bulbous mid-section but tapers gradually proximally and distally from that point. No basal pockets

or lobes. Ornamentation of both the asulcate and sulcate surfaces is similar. Basal area below the lobes with minute spines. At the level of the sulcus division the spines abruptly change to moderate sized, curved, mineralized spines. These spines continue to the tips of the lobes, gradually decreasing in size (i.e., proximal spines in this battery are the largest). Crotch of the organ between the lobes is nude, but distally the inner surfaces of the lobes are spinose. The lobes gradually taper toward their tips, which are blunt, with a few scattered minute spines (nearly nude), and rugose. Sulcus spermaticus a very deep groove with somewhat thickened borders. Spines present up to the edges of the sulcus. The sulcus ends in a dimple on the tip of each lobe where the retractor muscle attaches on the inside of the everted organ.

Coloration in Life (Holotype). Top of head somewhat reddish brown flecked with dark brown. Iris reddish brown or dull orange. Upper labials white, bordered above and below by a wavy dark brown or blackish line (Fig. 17). Rostral white; white irregular line extends from the rostral patch dorsally and posteriorly over the lateral edges of the internasals. Ventral surface of head dusky, heavily flecked with dark gray especially concentrated along the lip border, the mental scale, and genials; an irregular elongate white patch is present on each side of the throat on infralabials 4 and 5. The dark color of the ventral side of the head dissipates posteriorly, becoming a fine peppering over the entire venter concentrated toward the anterior edge of each ventral scale and denser on the anterior part of the body than more posteriorly. General aspect of venter light, washed with rose or pink. Nape collar orange dorsally, grading to dirty white on the side of the head; about three scales wide and extending from the posterior edge of the parietals onto the neck. Collar divided middorsally by a thin brown line extending from the parietals to the dark dorsal coloration on the body. Lateral

scales within the collar with dark brown spots occupying $\frac{1}{3}$ to $\frac{1}{2}$ of the area of each scale (Fig. 2); other collar scales more finely flecked with dark brown.

Middorsum dark brownish black, somewhat lighter laterally. Narrow reddish orange lateral stripe disposed as follows: anteriorly on row 5 followed by rows 5 and 6, then rows 4 and 5 (midbody), and rows 4, 5, and 6 (posteriorly); these changes generally correspond to the changes in dorsal row numbers. At the level of the vent the stripe continues uninterrupted onto the tail, broadening to occupy most of the lateral surface of the tail (although heavily suffused with dark brown) and continuing to its tip. The lateral pale stripe is bordered ventrally by a regular dark brown line 1–1.5 scales wide. The lower 2.5–3 dorsal rows are dirty white anteriorly but washed with reddish orange on the posterior $\frac{2}{3}$ of the body; these rows are flecked and spotted with dark brown.

The other adult male (MCZ 180299) was similar in coloration to the holotype, but the ventral wash was orangish rather than rose. The juvenile (MCZ 181287) was similar in coloration to the adults, but the nape collar and venter were white rather than orange or rose colored. Thus, like most species of *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994), *Pseudoxyrhopus oblectator* does not appear to undergo a significant ontogenetic change in coloration.

Coloration in Preservative. In preserved specimens, all the orange and rose colors fade to dirty white or pale brown and colors in general are duller.

HABITATS AND NATURAL HISTORY OF *PSEUDOXYRHOPUS OBLECTATOR*

All three specimens of *Pseudoxyrhopus oblectator* were collected during the rainy season at Ranomafana (roughly December–April). The holotype was found by day under a large log in relatively undisturbed upland primary rainforest. The juvenile (MCZ 181287) came from a hillside in selectively logged upland primary rainforest.

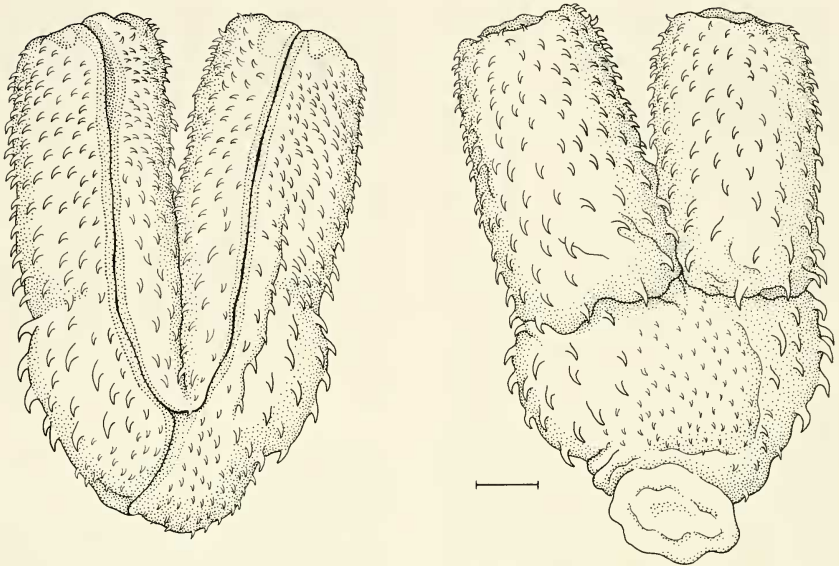


Figure 5. Hemipenis of *Pseudoxyrhopus oblectator* (holotype, MCZ 182292) in sulcate and asulcate views. Scale bar = 1 mm.

It was obtained from a drift fence and pit-fall trapline set parallel to a trail in an area of broken canopy at the forest/trail ecotone. The snake was retrieved from the trap in the morning and had probably fallen in the previous night. MCZ 180299 was dead on Route National 25, a small road passing through habitats similar to those in which the other specimens were found. *Pseudoxyrhopus oblectator* is most likely nocturnal and/or secretive, as are all other species of *Pseudoxyrhopus* for which observations on activity exist (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998).

Ranomafana National Park is divided by Route National 25 into a large northern sector and a smaller southern sector. The type locality of *Pseudoxyrhopus oblectator* is in the southeastern portion of the northern sector of the park, whereas the other two localities are in the southern sector in the vicinity of the Ranomafana Research Station at Talatahely (Fig. 3). The holotype

was obtained during a backpacking exploration of the course of the Ranomena River and its western tributaries, beginning at the village of Ambatolahy, traveling north to the western edge of the extensive riverine swamps along tributaries of the Ranomena River at approximately $21^{\circ}12'36''\text{S}$, $47^{\circ}26'\text{E}$ (indicated on the 1:50,000 Ifanadiana topographic map produced by FTM), and thence south and east following the main course of the river (Fig. 3).

The Ranomena River is a west-east flowing river of moderate size that joins the Tsaratango River near the village of Bevohazo (the Ranomena River should not be confused with the Menarano River in the southern sector of Ranomafana National Park; both names mean "red water," referring to the dark rusty color of these blackwater streams). At approximately $21^{\circ}13'07''\text{S}$, $47^{\circ}27'10''\text{E}$, the Ranomena River passes over an escarpment with huge

boulders, cascading waterfalls, and an abrupt drop in elevation. The type locality of *Pseudoxyrhopus oblectator*, along a small tributary of the Ranomena River called *Mahajo* (pronounced Mah-hah'-zhū) by local informants, is a short distance east of this precipice and south of the main course of the Ranomena River. The Mahajo ascends rather steeply away from the Ranomena River in this hilly terrain.

At the type locality Mahajo Stream is very shallow, amounting to rivulets of less than 30 cm basal depth (when not swelled by rains) meandering among boulders. It is 2–4 m wide, with white water and a substrate of sand, gravel, and scattered boulders. Slopes away from the stream are steep, well drained, and covered with forest containing many tree ferns, few *Pandanus* (Pandaceae), and many hardwoods, principally *Ocotea* (Lauraceae) and trees referred to by their Malagasy names *maka* (probably *Dombeya* sp. [Sterculiaceae]; Heckel, 1910) and *tsinkotroka* (Melastomataceae; probably *Dichaetanthera* sp.; Heckel, 1910). Very few polysandra (*Dahlbergia* sp.), a major commercial hardwood, were present, probably because of prior and continuing exploitation of this tree in the area. Habitats at the localities where the other two specimens were taken are similar to those at the type locality but slightly more disturbed by old (>50 years) selective logging. All three localities are characterized by steep, well-drained slopes and have whitewater streams in the uplands, although the two major rivers near the known localities (the Ranomena and the Namorona) are blackwater. None of the specimens of *Pseudoxyrhopus oblectator* was closely associated with streams.

One dietary record is available for *Pseudoxyrhopus oblectator*. The juvenile (MCZ 181287; SVL = 143 mm, head width = 5.1 mm) had eaten five eggs of *Amphiglossus melanopleura* (Squamata: Scincidae) containing full-term embryos. All embryos were within their shells (egg diameters 5.75–6.25 mm), fully developed (with

complete pigmentation), and probably close to hatching; two embryos removed from their shells for identification still had hemipenes everted. This probably constitutes one entire clutch of eggs; two gravid females of *A. melanopleura* from the Ranomafana area contained four and five shelled eggs, respectively (personal observations; a large clutch size for such small lizards!).

Neither of the two specimens of *Pseudoxyrhopus oblectator* collected alive showed any attempt to bite or struggle significantly. This behavior is similar to that of all specimens of *P. tritaeniatius* that I have observed alive—they are docile, inoffensive snakes and often slow moving even when handled.

HEMIPENIAL MORPHOLOGY OF *PSEUDOXYRHOPUS*

No hemipenes of *Pseudoxyrhopus* have been described previously. In addition to *Pseudoxyrhopus oblectator*, I examined hemipenes of three other species in detail: *P. ambreensis* (UMMZ 200061; everted), *P. sokosoko* (UMMZ 209689; in situ, retracted), and *P. tritaeniatius* (MCZ 182468; everted). A hemipenis of *P. kely* (UMMZ 192022; in situ, retracted) was examined externally for proportions only. This specimen, a paratype of *P. kely*, was reported as a female by Raxworthy and Nussbaum (1994), but its hemipenes are evident through a previous slit in the tail and small, immature testes are visible through a previous slit in the body. The specimens of *P. sokosoko* and *P. kely* are juveniles; the others are adults.

Hemipenes of all species are very similar in overall morphology, ornamentation, and sulcus position. The description given for the hemipenis of *P. oblectator* (Fig. 5) could suffice as a general description for any of the other species examined in detail except for slight proportional differences. In fact, the detailed similarity among the species is quite remarkable. The tips of the sulcus spermaticus appear to end in a dim-

ple in three species (*P. oblectator*, *P. tritaeniatus*, and *P. ambreensis*; configuration unclear in the retracted juvenile organ of *P. sokosoko*). This somewhat unusual feature may be characteristic of the genus; it does not appear to be an artifact of incomplete eversion.

The hemipenis of *Pseudoxyrhopus ambreensis* is 10.5 mm total length and bilobed for the distal 4.5 mm (43% bilobed). The hemipenis of *P. tritaeniatus* is 17 mm total length and bilobed for the distal 5 mm (29% bilobed). Of the species examined, the hemipenis of *P. tritaeniatus* has a more bulbous midsection and the shortest lobes. The retracted hemipenis of *P. sokosoko* extends to the level of the suture between subcaudals 4 and 5, dividing about the middle of subcaudal 2 (total length 4.6 mm, bilobed for the distal 3 mm [65%]). The spine ornamentation in *P. sokosoko* appears similar to that in the other species, although because the specimen is a juvenile the spines are nonmineralized and the specific pattern is difficult to discern. The retracted left hemipenis of *P. kely* extends to the level of the suture between subcaudals 5 and 6, dividing at the level of the suture between subcaudals 2 and 3 (total length 3.4 mm, bilobed for the distal 1.8 mm [53%]).

Although it is difficult to compare proportions of everted and retracted hemipenes, *Pseudoxyrhopus oblectator*, *P. kely*, and *P. sokosoko* have more deeply bilobed hemipenes (53–65%) than do the other two species (29–43%).

MAXILLARY TOOTH FORMULAE IN *PSEUDOXYRHOPUS*

Raxworthy and Nussbaum (1994) recognized four species groups of *Pseudoxyrhopus* (A–D) based on characters of the maxillary and dentary dentition and later included body size and the number of dorsal, ventral, and subcaudal scales in group definitions (Nussbaum et al., 1998). Although these groups were stated to be explicitly phenetic, Raxworthy and Nuss-

baum (1994) and Nussbaum et al. (1998) used the group characters to infer relationships among the species of *Pseudoxyrhopus*. My study revealed several characters recorded erroneously by previous authors. In this and the next sections I correct these observations, reinterpret several characters, and point out additional characters that may bear on relationships within *Pseudoxyrhopus*. I revisit relationships hypothesized by Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998) in the context of evaluating the relationships of *Pseudoxyrhopus oblectator*.

A character used by Raxworthy and Nussbaum (1994) to distinguish species in Group A from the others was the presence of only a single enlarged posterior maxillary fang rather than two. I am aware of no other rear-fanged colubrids reported to have a single rear fang (or socket), although three fangs are present in some species (e.g., *Boiga* species; see, Bogert, 1940) and multiple enlarged rear teeth are present in some species of *Liophidium*. Because *Pseudoxyrhopus oblectator* has two enlarged posterior maxillary teeth but is otherwise very similar to *P. ambreensis* (Group A), I reevaluated the dental characters of the species readily available (Table 2). My reevaluation suggests that interpretations of a single posterior maxillary fang in two species of Group A (*P. ambreensis*, *P. kely*) are erroneous. The same is probably true of the other species of Group A (*P. analabe*), but the only known specimen has not been reexamined.

Based on UMMZ 200061, Raxworthy and Nussbaum (1994: 4) reported the maxillary dentition of *Pseudoxyrhopus ambreensis* as “12+1 maxillary teeth, the posteriormost tooth considerably enlarged and separated by a gap from the anterior 11 teeth.” They indicated that *P. ambreensis* was “unusual compared to most other *Pseudoxyrhopus* species in that there is just a single enlarged posterior maxillary tooth rather than two.” This was the con-

TABLE 2. DENTITIONAL VARIATION AMONG SPECIES OF *PSEUDOXYPHOPUS*. FEWER DENTARIES WERE EXAMINED THAN MAXILLAE.

Species	Maxillary teeth		Dentary teeth		Maxillary diastema	
	Formula ¹	n ²	Formula ¹	n	Size ¹	n
<i>P. ambreensis</i>	15+2	2	5 (6-8) D10 = 18	1	absent	1
	14+2	1			= 1 tooth	1
	13+2	1			≤ 1 tooth	1
<i>P. imerinac</i>	13+2	1	5 (6-8) D10 = 18	1	absent	1
<i>P. kely</i>	12+2	1	4 (5-7) DS = 15	1	absent	1
<i>P. microps</i>	17+2	1	5 (6-8) D12 = 20	1	absent	1
<i>P. oblectator</i>	17+2	1	6 (7-9)-5 = 17 ¹	1	absent	1
	16+2	2				
	14+2	1				
<i>P. quinquelincatus</i>	14+2	2	5 (6-8) D7 = 15	2	absent	2
	13+2	4	5 (6-8) DS = 16	1	= 1 tooth	1
			5 (6-7) DS = 15	1	> 1 tooth	2
		4 (5-7) DS = 15	1			
<i>P. sokosoko</i>	12+2	1	5 (6-8) D10 = 18	1	= 1 tooth	1
	15+2	1			≤ 1 tooth	1
<i>P. tritaeniatus</i>	15+2	2	5 (6-8) D13 = 21	3	absent	1
	16+2	3	5 (6-8) D12 = 20	1	≤ 1 tooth	2
					< 1 tooth	1

¹See Materials and Methods for explanation of scores.

²Number of specimens having a particular formula or diastema condition; these include observations made bilaterally on the same specimen (e.g., for skulls).

¹Diastema variable.

dition later reported for *P. kely* and *P. analabe* (Raxworthy and Nussbaum, 1994: 14; Nussbaum et al., 1998: 130). These observations for *P. ambreensis* and *P. kely* are inaccurate. On the left side of UMMZ 200061 both fangs are still in place, although the posterior one is loose; on the right side, the anterior fang is missing and its empty socket is presumably the "gap" reported by Raxworthy and Nussbaum (1994); no diastema is present. Anterior to the pair of rear fangs in each maxilla of UMMZ 200061 are 15 teeth. The difference between my counts and those previously reported for this specimen (Raxworthy and Nussbaum, 1994) is probably due to failure to count empty tooth sockets or the small teeth at the anterior ends of the maxillae, which are easy to miss in small snakes. In general, my tooth counts are somewhat greater than those given by Raxworthy and Nussbaum (1994) when we have examined the same specimens. Thus, the correct maxillary tooth formula for UMMZ 200061 is 15+2 on each side.

At my request the maxillary fangs of the holotype of *Pseudoxyrhopus kely* (UMMZ 192021) were rechecked and Greg Schneider (in litt.) reported that the left side has two enlarged rear fangs, whereas the right side has one fang plus an empty socket. The paratype of *P. kely* (UMMZ 192022), which I examined, has a posterior fang in place on each maxilla and an empty socket for the other fang. Thus, I conclude that all species of *Pseudoxyrhopus* of Group A have the usual condition of two posterior fangs, in contrast to the claim that the group is characterized by a single fang.

Nonetheless, Group A of *Pseudoxyrhopus* is still characterized by the combination of relatively small size, low numbers of ventral and dorsal scales, fewer than 12 posterior dentary teeth, and a pale nuchal band (Nussbaum et al., 1998). However, none of these characters individually is unique to Group A and only the pale nuchal band distinguishes it from Group B. By these criteria *P. oblectator* belongs to phenetic Group A.

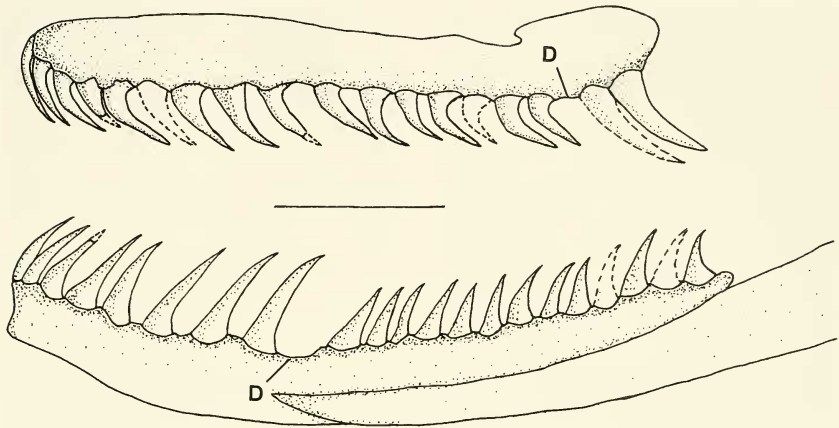


Figure 6. Left maxilla and right dentary (reversed) of *Pseudoxyrhopus tritaeniatus* (MCZ 182468). *D* = the diastemata in each tooth row. Teeth drawn with dotted lines are missing. Scale bar = 3 mm.

MAXILLARY AND DENTARY DIASTEMATA IN THE *PSEUDOXYRHOPUS* GROUP

In *Pseudoxyrhopus oblectator* the gap separating the anterior rear fang from the last small maxillary tooth is less than half the width of the tooth and approximately equivalent to the space between adjacent teeth in the rest of the maxilla (Fig. 4). Based on the criterion outlined *P. oblectator* lacks a diastema, a condition different from that reported for all other species of *Pseudoxyrhopus* (e.g., see Boulenger, 1890, 1893; Mocquard, 1909; Guibé, 1958; Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). Presence of a diastema is usually stated as a generic character for *Pseudoxyrhopus* (Boulenger, 1893; Raxworthy and Nussbaum, 1994). Thus, I re-examined the diastema in other readily available species of *Pseudoxyrhopus*.

In seven species of *Pseudoxyrhopus* studied, a maxillary diastema is either absent (some *P. ambreensis*, *P. kely*, *P. microps*, *P. oblectator*, some *P. quinquelineatus*) or very narrow (approximately equal to the width of a single tooth or less; some

P. ambreensis, some *P. quinquelineatus*, *P. sokosoko*, *P. tritaeniatus*; Fig. 6). The broadest diastemata observed, 1–1.5 times the width of a tooth, were in two specimens of *P. quinquelineatus*.² Boulenger (1890), using crude diagrams, illustrated a maxillary diastema approximately the width of two teeth for *P. inerinae*, *P. microps*, and *P. quinquelineatus*. However, I examined maxillary dentition of all three species (Table 2) and each differs from Boulenger's illustrations. Both *P. microps* and *P. inerinae* lack a diastema, the space in front of the anterior fang being less than

² Charles W. Myers (in litt.) pointed out to me that some of the variation in diastema width could reflect differences in the number of pre-diastemal teeth—the more teeth the shorter the diastema within a species. My samples for species of *Pseudoxyrhopus* are too small to evaluate this hypothesis, but it does not seem to hold in *P. quinquelineatus*, for which six maxillary tooth counts varied only from 13 to 14 + 2. The broadest diastema (1.25–1.5 times tooth width) was in one specimen with 13 pre-diastemal teeth, whereas three other specimens with 13 teeth had no diastema. Nevertheless, the relationship between tooth numbers and diastema width bears additional (and more quantitative) study.

the width of a tooth. Variation in the width of the diastema is greatest among specimens of *P. quinquelineatus*. In this species the width of the diastema varies from less than one tooth to approximately 1.5 teeth. Of course, differences between Boulenger's observations and mine could represent intraspecific variation (or simply the crudeness of Boulenger's diagrams). However, given that the width of the diastema varies intraspecifically in *P. ambreensis* and *P. quinquelineatus* (Table 2), other species may vary as well (aside from *P. quinquelineatus* no species is represented by more than three observations). In all species of *Pseudoxyrhopus* the impression of a diastema is created by the posterior projection of the fangs adjacent to the vertically projecting teeth anterior to them (Figs. 4, 6). Detailed examination of the tooth bases is necessary for proper interpretation of the diastema. This morphology and the mistaking of empty sockets for a diastema probably account for previous recordings of a diastema in all species of *Pseudoxyrhopus* (e.g., Raxworthy and Nussbaum, 1994).

All species of *Pseudoxyrhopus* for which the dentary teeth were examined (*P. ambreensis*, *P. imerinae*, *P. kely*, *P. microps*, *P. oblectator*, *P. quinquelineatus*, *P. sokosoko*, *P. tritaeniatus*; Table 2) and "*Pararhadinaea*" *albignaci* have a previously unreported short diastema in the dentary tooth row separating the last of the median enlarged teeth from the following series of small dentary teeth (Fig. 6). Such a diastema was not present in *Heteroliodon occipitalis*. In *Pararhadinaea melanogaster*, the posterior four or five dentary teeth are separated by broad spaces, although none is discrete enough to be called a diastema.

The dentary diastema in *Pseudoxyrhopus* ranges from slightly smaller to slightly greater than the width of the large tooth preceding it but is always clearly larger than the spaces between the other dentary teeth. The diastema was narrowest in *P. oblectator*, in which a narrow dentary diastema was present in the holotype but not

in the prepared skull of MCZ 180299. Thus, this character may vary intraspecifically (in general, I had only a single observation per species), although each of six dentaries (four specimens) of *P. quinquelineatus* had a distinct dentary diastema. Diastemata are not common in colubrid dentary tooth rows, although very broad ones are found in some, such as *Lycophidion* (Parker, 1933; Savitzky, 1981) and *Lycodon* (Smith, 1943).

Some variation in tooth form and proportions exists among species of *Pseudoxyrhopus*. For example, in the large species, *P. tritaeniatus* and *P. microps*, the teeth are relatively longer, more strongly curved, and more sharply pointed than in the smaller species (cf. Figs. 4, 6). In *P. tritaeniatus* the anterior maxillary teeth are slightly longer than the posterior ones (excluding fangs) (Fig. 6), whereas the opposite trend occurs in other species (e.g., *P. quinquelineatus*), and maxillary teeth are more or less subequal in still others. The fangs of all species of *Pseudoxyrhopus* are compressed to a greater or lesser extent, with a rounded anterior edge tapering to a narrow posterior edge. In some species the posterior edges of the fangs bears a slightly raised keel (e.g., *P. tritaeniatus*), whereas in others a broad knifelike ridge occurs posteriorly (e.g., *P. oblectator*, *P. ambreensis*).

All species of *Pseudoxyrhopus* examined have three distinctly enlarged median dentary teeth (Table 2), a character used in part to diagnose *Pseudoxyrhopus* (Boulenger, 1893; Raxworthy and Nussbaum, 1994). In most species these teeth are distinctly larger than the teeth anterior and posterior to them. However, in *P. tritaeniatus* the enlarged dentary teeth are not so distinguished in size from the anterior teeth (Fig. 6) (in the *P. microps* examined the anterior dentary teeth were missing). This size similarity results from the fact that the anterior dentary teeth are already large and the transition to enlarged teeth occurs in the first two or three teeth in the series. Thus, in *P. tritaeniatus* the distinc-

tion between the enlarged dentary series and the more anterior teeth is arbitrary. The same pattern of relative tooth size especially enhances the size distinction between the anterior (large) and posterior (small) dentary teeth in *P. tritaeniatus* (Fig. 6). Although the size difference between the anterior and posterior dentary teeth is sometimes stated as a "generic character" in *Pseudoxyrhopus* (e.g., Raxworthy and Nussbaum, 1994), it is most apparent in the large species and may not be evident at all in the small ones.

RELATIONSHIPS OF *PSEUDOXYRHOPUS OBLECTATOR* AND A RECONSIDERATION OF SPECIES GROUPS WITHIN *PSEUDOXYRHOPUS*

Nussbaum et al. (1998) characterized *Pseudoxyrhopus* species Group A (including *P. ambreensis*, *P. kely*, and *P. analabe*) as follows:

small size (<235 mm SVL), low numbers of scale rows (19 or 21), low numbers of ventral (<154) and subcaudal (<54) scales, fewer than 12 dentary teeth posterior to the largest dentary tooth, a single enlarged posterior maxillary tooth, and a pale nuchal band.

The size range is an error because according to their own data (Nussbaum et al., 1998, table 1) *P. ambreensis* reaches 333 mm SVL. When corrected to reflect the presence of two rather than one fang, *Pseudoxyrhopus oblectator* conforms to this definition except for a slight difference in ventral count. The other species groups differ by lacking a nuchal collar (Group B), having more than 12 posterior dentary teeth, more dorsal scale rows, larger size, and more ventrals and subcaudals (Group C), or having a pointed snout and strongly overhanging rostrum (Group D).³ How-

ever, there is no reason to expect that all these groups actually reflect nearest relationships. Groups A and B, for example, are distinguished only by the presence (A) or absence (B) of a pale nuchal collar.

As pointed out in the diagnosis, *Pseudoxyrhopus oblectator* is most similar to *P. ambreensis* (Group A) and *P. sokosoko* (Group B). *Pseudoxyrhopus ambreensis*, known only from extreme northern Madagascar (Fig. 3), is geographically remote from *P. oblectator* and *P. sokosoko* and differs from them in the disposition of the pale lateral stripe and in having a less divided hemipenis. However, the close similarity of *P. oblectator* and *P. sokosoko* (Group B) raises the possibility that these two are sister species, although any such suggestion is based on shared characters of uncertain polarity. The only substantive difference between *P. oblectator* and *P. sokosoko* is the presence (*P. oblectator*) or absence (*P. sokosoko*) of a nuchal collar. The two species are virtually identical in

showed 12 posterior dentary teeth [18 total] for each species). My observations for these species differ. Four specimens of *P. quinquelineatus* (six dentaries, including two prepared skulls) have either seven or eight posterior dentary teeth, and one specimen of *P. ineriniae* had 10 posterior dentary teeth (Table 2). Boulenger's (1890) primary concern was calling attention to the anterior enlarged dentary teeth in *Pseudoxyrhopus*. As suggested elsewhere with respect to the maxillary diastema, his figures are highly diagrammatic and may not be accurate with respect to tooth number and placement, as suggested, for example, by the wide spacing among the anterior dentary teeth in Boulenger's diagrams and his failure to indicate the dentary diastema that is present in each of these species. Given the highly schematic nature of these figures, Boulenger may have intended to show the general pattern and not the precise count of the posterior dentary teeth. In any case, whether the variation were 7–12 posterior dentary teeth, or some smaller variance around 7, this character does not apply to define Group D as used by Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998). Although the number of dentary teeth is expected to vary just as maxillary tooth number, an intraspecific range of 7–12 posterior teeth seems large. However, *P. ineriniae* and *P. quinquelineatus* have a pointed overhanging snout and unusual color pattern relative to other species of *Pseudoxyrhopus*, which suggests that they are sister species.

³ Group D includes *Pseudoxyrhopus ineriniae* and *P. quinquelineatus*. Based on Boulenger's (1890) illustrations of dentition in these species, Raxworthy and Nussbaum (1994) and Nussbaum et al. (1998) included the presence of 12 or more posterior dentary teeth in the definition of Group D (Boulenger

the disposition of the pale lateral stripe, they have the most deeply bilobed hemipenes of the species examined (58% and 65%, respectively), and they are similar in size, scale counts, and color pattern (except for the collar). *Pseudoxyrhopus sokosoko* is known from extreme southeastern Madagascar (Fig. 3) from lower elevations (≤ 800 m) than is *P. oblectator* (>900 m).

Pale nuchal collars are probably plesiomorphic within *Pseudoxyrhopus* inasmuch as collars are present in the presumed close relatives, *Heteroliodon*, "*Pararhadinaea*" *albignaci*, and *Pararhadinaea melanogaster*, and in 7 of the 11 species of *Pseudoxyrhopus* (in *P. microps* collars are present only in juveniles, and in *P. tritaeniatus* collars are variably present). Thus, the sharing of a collar by species of Group A provides no clear evidence of relationship. Because this character is the only one distinguishing Groups A and B, evidence for the interrelationships of these species must be sought in other characters. If *P. sokosoko* and *P. oblectator* are sister species and the interpretation of collars as plesiomorphic within *Pseudoxyrhopus* is correct, then collars have been lost independently in *P. sokosoko* and the other species of *Pseudoxyrhopus* that lack collars.

In contrast, Raxworthy and Nussbaum (1994) proposed that *Pseudoxyrhopus sokosoko* and *P. heterurus*, a widespread species of the eastern rainforests, are sister species comprising Group B. These species lack nuchal collars and have 21 scale rows, fewer than 12 posterior dentary teeth, and two enlarged maxillary teeth. Twelve or fewer posterior dentary teeth is a character also shared by the four species of Group A and other species, including at least *P. imeriniae* and *P. quinquelineatus* (see footnote 3, Table 2). The other characters are widespread or universal within the genus. *Pseudoxyrhopus heterurus* differs from *P. sokosoko* in lacking a lateral stripe and having undivided anterior subcaudal scales and a larger body size. How-

ever, in *Pseudoxyrhopus heterurus* and *P. analabe* (Group A; Nussbaum et al., 1998) the subcaudals are wholly or partially undivided, an unusual (for colubrids) and ostensibly derived character that might indicate close relationship. This character argues more strongly for a *P. heterurus*-*P. analabe* relationship than do the characters linking *P. heterurus* and *P. sokosoko*.

Data presented herein challenge the maxillary and dentary tooth formulae originally used to characterize the species groups of *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). I suggest that some other characters (presence of a collar) are plesiomorphic and thus provide no evidence of relationship and that some other characters (entire subcaudals) bear further scrutiny for elucidating relationships within *Pseudoxyrhopus*. Any hypothesis of relationships within *Pseudoxyrhopus* currently depends on the relative significance attributed to characters such as the nuchal collar, lateral stripes, and scutellation differences. Certainly, with the revised definition of Group A proposed herein, the distinction between Groups A and B seems arbitrary. However, the case for considering *P. imeriniae* and *P. quinquelineatus* sister taxa seems secure because they share an unusual snout form and color pattern within *Pseudoxyrhopus*. Likewise, several characters shared by *P. tritaeniatus*, *P. ankafinaensis*, and *P. microps* seem to be apomorphic, thus supporting recognition of this group (Group C of Nussbaum et al., 1998) as a clade. However, the apomorphic nature of these shared characters is apparent only after proper interpretation of other dental characters of *Pseudoxyrhopus* and its relatives, which is the focus of the remainder of this report.

HINGED TEETH AND OTHER DIETARY SPECIALIZATIONS IN THE *PSEUDOXYRHOPUS* GROUP

Hinged Teeth

Among snakes hinged teeth have been previously reported in *Xenopeltis* (Xeno-

peltidae) and a small number of colubrid genera in the Neotropics, Africa, Madagascar, and southeast Asia (*Scaphiodontophis*, *Mehelya*, *Liophidium*, *Lycophidion*, *Sibynophis*, *Iguanognathus*) (Savitzky, 1981; Jackson et al., 1999).⁴ In such teeth a fibrous connection between the base of each tooth and the jaw bone allows the teeth to be folded down. Their occurrence is correlated with a diet of hard-bodied lizard prey, such as skinks and gerrhosaurids (Savitzky, 1981, 1983). Among Malagasy snakes hinged teeth have previously been reported in several species of *Liophidium* (Savitzky, 1981). I here report their presence in *Pseudoxyrhopus*, *Pararhadinaea melanogaster*, "*Pararhadinaea*" *albignaci*, and *Heteroliodon occipitalis*. Detailed discussion of dentition in the last three is deferred to subsequent sections. In *Pseudoxyrhopus* hinged teeth are present in all

species examined, but in *P. tritaeniatus* hinged teeth seem to be present in juveniles but not in the adults examined.⁵

These observations were prompted by examination of the maxillary dentition of the holotype of *Pseudoxyrhopus oblectator*, in which the teeth anterior to the fangs fold backward when pressed from the lateral or anterior surface with a needle. The dry skull of *P. oblectator* (MCZ 180299) is missing many of its teeth, but those that remain are detached on the anterobasal edge and deflected posteriorly; they appear to be attached basally on their posterior edges (Fig. 4). This configuration is very similar to that depicted for *Xenopeltis unicolor* and *Scaphiodontophis annulatus* (Savitzky, 1981, figs. 1C,G). The missing teeth of MCZ 180299 were probably lost because of their loose attachment at the jaw line and perhaps some deterioration prior to preservation (this snake was a roadkill). Using a fine needle as a probe, similarly mobile teeth were also found in *P. ambreensis*, *P. imerinae*, *P. kely*, *P. quinquelineatus*, and *P. sokosoko*. The specimen of *P. microps* examined was poorly preserved and had many teeth missing, but the anterior teeth in both the maxilla and dentary appeared to be somewhat kinetic, whereas posterior teeth were less so or even akinetic. Adults of *Pseudoxyrhopus tritaeniatus* appear not to have dental kinesis at all. In adult fluid-preserved specimens and dry skulls of this species the teeth are firmly ankylosed to the bones. However, dental kinesis was evident in a small juvenile of *P. tritaeniatus* (AMNH 60712; SVL 270 mm). To convince myself that the kinesis I observed in *Pseudoxyrhopus* was not some peculiar artifact of preservation I manipulated the dentition of many specimens of species in other

⁴ Hinged teeth may be more widespread than realized among colubrids. Inspired by Parker's (1933) discussion of *Lycophidion* and *Chamaelycus* (= *Oophilosotum* Parker), I inspected teeth in specimens of *Chamaelycus* and its presumed close relatives, *Hornonotus* and *Gonionotophis*, in addition to *Lycophidion* and *Mehelya* (see Savitzky, 1981). These genera comprise Group II of Bogert (1940). *Chamaelycus fasciatus* (MCZ 11165, 49605, 53461) and *C. parkeri* (MCZ 42657) also appear to have hinged teeth, whereas *Hornonotus modestus* (MCZ 5649, 22510) and *Gonionotophis granti* (MCZ 51813, 55355; MVZ 176439) do not. Parker (1933) reported two unidentified lizard eggs and Ineich (1998) reported a *Gerrhosaurus nigrolineatus* in stomachs of *Chamaelycus fasciatus*.

Edmond V. Malnate (in litt.) informed me that the Asian natricines *Amphiesma celebica* and *Tropidonophis truncatus* were skink feeders, and at his suggestion I examined the teeth of these species (MCZ 25267-69 and MCZ 33508, respectively). The teeth in both species are slightly blunt, which Malnate and Underwood (1988) suggested might be related to a diet of lizards with heavy osteoderms. In *A. celebica* a few teeth in the middle of the maxilla seemed to be hinged, but the three specimens examined had many missing teeth. However, in *T. truncatus* the teeth on approximately the anterior two-thirds of the maxilla are hinged. Thus, hinged teeth and other dental characters discussed herein are geographically widespread characters of colubrids feeding on lizards with dense osteoderms and have clearly evolved multiple times in the context of similar dietary regimes.

⁵ Determination of dental kinesis must be done with fluid-preserved specimens. In dry skulls kinesis may be indicated by peculiar deflection of some teeth (e.g., Fig. 4) or by the appearance of an abscission line at the base of the teeth, but both of these features vary among preparations.

Malagasy colubrid genera collected on the same and different field trips as the *Pseudoxyrhopus*. In no case did I observe dental kinesis nor a modified tooth replacement (except in *Liophidium*), as observed in *Pseudoxyrhopus*.

The similarity of kinetic teeth (in fluid-preserved specimens) or anterobasally detached teeth (in dry skulls) in *Pseudoxyrhopus* and other hinge-toothed snakes (Savitzky, 1981) strongly suggests that the teeth of these species of *Pseudoxyrhopus* have a similar hinge mechanism (the connective tissue hinge is visible in histological and electron microscopic preparations). With few exceptions, the hinged condition in *Pseudoxyrhopus* appears to apply to all maxillary teeth except the fangs and to all dentary teeth except the median series of enlarged teeth, which are firmly ankylosed to the bone. In the dry skull of *P. oblectator* (MCZ 180299) the palatine and pterygoid teeth also appear to be hinged because they are detached anterobasally, just as the maxillary and dentary teeth. Palatine and pterygoid dental kinesis was also evident in a juvenile specimen of *P. tritaeniatus* (AMNH 60712). In several specimens my subjective impression was that the anterior maxillary and dentary teeth were more kinetic than were more posterior teeth, especially those immediately anterior to the fangs. The tendency for more kinetic teeth to occur anteriorly in the jaw may make functional sense if these are the first teeth to engage struggling prey.

In *Pseudoxyrhopus*, *Heterohiodon*, "*Pararhadinaea*" *albignaci*, and *Pararhadinaea melanogaster* the extent of posterior deflection permissible in the kinetic teeth seems to be at most about a 20–30° arc, which is insufficient to allow the teeth to lie in a horizontal plane. This is approximately equivalent to or slightly less than the extent of dental kinesis produced by similar manipulation of preserved specimens of *Liophidium torquatum*, *L. rhodogaster*, *L. vaillanti*, and several species of *Lycophidion* and *Mehelya* (personal ob-

servations of MCZ specimens). The small degree of dental kinesis contrasts with the condition in some other hinge-toothed snakes such as some species of *Liophidium* and *Scaphiodontophis*, in which the teeth can be folded completely to the jaw line (Savitzky, 1981) (as a caveat, the effect of preservational differences on this character is unknown). However, even in *Liophidium* the degree of dental kinesis seems to vary among species. For example, *L. vaillanti* and *L. torquatum* seem to have less kinetic teeth than does *L. rhodogaster* (Savitzky, 1981; personal observations). Even greater variation in tooth kinesis exists between the three previously recognized groups of snakes having hinged teeth (Savitzky, 1981). Such variation in dental kinesis appears to obtain in *Pseudoxyrhopus* as well, with some species having well-developed kinesis and adults of at least one species lacking it entirely.

In overall tooth morphology and degree of specialization the hinged teeth of *Pseudoxyrhopus* appear more similar to those of Group 3 of Savitzky (1981), including the African genera *Lycophidion* and *Mehelya*, than to those of Group 2, including *Liophidium* (Madagascar), *Scaphiodontophis* (Central America), and *Sibynophis* (southeast Asia).⁶ In general, species of Group 3 are less specialized and their teeth are less kinetic than those of Group 2. Species in Group 2 often have distally compressed, sometimes spatulate, teeth that are attached to the bone via a well-defined, thickened pedicel. In contrast, the teeth of Group 3 are more typical in overall morphology, their hinges appear to be less fully developed, and they do not have distinct pedicels. *Pseudoxyrhopus* fits the general pattern of Group 3. However,

⁶ Savitzky's (1981, 1983) groups were intended to imply morphological and functional similarity and not necessarily phylogenetic relationship. He suggested that the genera of Group 2 were probably not closely related, implying independent origins of the tooth specializations within this group. However, he conjectured that *Lycophidion* and *Mehelya* (Group 3) were, in fact, close relatives (see also Bogert, 1940).

the teeth of *Heteroliodon* and *Pararhadinaea melanogaster* have an unusual morphology similar to that of the teeth of Group 2 snakes.

Modified Tooth Replacement

Savitzky (1981) observed that the typical snake pattern of alternate tooth replacement had been modified or abandoned in the other hinge-toothed snakes (see also Leviton, 1964; Morgan, 1973). This may be the case in *Pseudoxyrhopus*; tooth-bearing bones in these species typically have few empty sockets (aside from damaged or deteriorated specimens) and adjacent teeth are similarly kinetic or (in *P. tritaeniatus*) firmly ankylosed. In contrast, in most colubrids sockets that are empty or that have loose replacing teeth roughly alternate with sockets occupied with firmly ankylosed teeth (best assessed with fluid-preserved specimens rather than dry skulls). In *P. ambreensis*, *P. quinquelineatus*, and *P. sokosoko* a tendency toward alternating teeth was more evident on the posterior half of the maxilla (missing teeth were usually posterior ones), whereas the anterior maxillary teeth were nonalternating. This pattern corresponds to a subjective impression of greater kinesis in the anterior teeth than in the posterior ones and suggests a change of tooth replacement mode within the maxilla. Significantly, even *P. tritaeniatus* appears to show modified tooth replacement even though its teeth do not appear to be hinged in adults (the specimen of *P. microps* examined retained too few teeth to evaluate this character; this snake seems to have died some time before preservation, and most teeth were missing).

The precise nature of the modified tooth replacement observed in *Liophidium*, *Pseudoxyrhopus*, and related genera is uncertain and needs additional study. Morgan (1973), commenting on tooth replacement in several genera subsequently discovered to have hinged teeth, remarked that *Scaphiodontophis* had "simultaneous" (as contrasted with alternate) tooth re-

placement, but he saw nothing unusual in the replacement patterns of *Liophidium* or *Sibynophis*. However, he was unaware of the unusual hinge attachment of the teeth in all of these genera subsequently discovered (Savitzky, 1981). Savitzky (1981: 348) interpreted the presence of functional teeth in most sockets in *Liophidium* and other genera as evidence of "abandonment or modification of alternate tooth replacement" in these genera. I have made a similar inference for the genera under study herein. But it seems clear that the story is not so simple. Most species have been studied only as dry skulls, which except in special circumstances do not permit examination of tooth replacement directly.

Savitzky (in litt., 16 November 1998) indicated that the observation of functional teeth in most sockets suggests "not so much that alternate tooth replacement is utterly lost as that the process is much more rapid, since bone of attachment needn't be laid down." That is, the fibrous hinge attaching the teeth, which develops relatively early in replacement teeth (Savitzky, 1981), permits more rapid tooth replacement than seen typically in colubrids. The end result is that most tooth sockets in the hinge-toothed snakes have functional teeth. Regardless of the precise pattern or mechanism of tooth replacement, all the genera under study herein have a high frequency of filled tooth sockets, which I interpret to reflect some modification of the underlying pattern of tooth replacement.

DENTITION AND PREY IN *PSEUDOXYPHOPUS* AND RELATED GENERA, WITH A CRITIQUE OF SPECULATIONS ON THE DIETS OF THESE AND OTHER SNAKES

Several peculiar features of the dentition of *Pseudoxyrhopus*, *Heteroliodon*, and *Pararhadinaea* are seen in other snakes that feed on skinks and gerrhosaurids. These lizards have well-developed osteoderms underlying the scales that when combined with smooth scales and highly

muscular bodies, pose difficulties for capture by snakes (Parker, 1933; Vitt et al., 1977; Savitzky, 1983; Greene, 1989a). Hinged teeth are the most obvious dietary specialization in snakes for these prey, but other characters observed in these species are also frequently associated with this diet (Parker, 1933; Savitzky, 1983; Greene, 1989a, 1997). These characters include (1) the enlarged median series of dentary teeth and/or the dentary diastema observed in *Pseudoxyrhopus*, "*Pararhadinaea*" *albignaci*, and *Heteroliodon* and (2) enlarged median maxillary teeth and an exceptionally broad maxillary diastema separating enlarged maxillary teeth in "*Pararhadinaea*" *albignaci*.

No dietary data are available for these snakes except *Pseudoxyrhopus*, for which two food records are available in addition to the *Amphiglossus melanopleura* eggs reported for *P. oblectator*. Raxworthy and Nussbaum (1994) reported a specimen of *P. kely* (UMMZ 192022; SVL 130 mm) that contained an adult *A. melanopleura*. The intestine of an adult *P. tritaeniatus* (MCZ 182480; SVL 782 mm) from the Ranomafana National Park was packed with fine reddish brown hair that probably belonged to a *Nesomys rufus* (Rodentia: Muridae: Nesomyinae). The identity of the prey is inferred from the distinctively colored fur of this rat and the lack of clear alternatives in a reasonably well-known small mammal fauna (James Ryan, G. Kenneth Creighton, and Louise H. Emmons, unpublished mammal checklist for Ranomafana National Park).

Predation on reptile eggs as reported here for *Pseudoxyrhopus oblectator* is uncommon in snakes, but even many snakes considered to be reptile egg specialists consume lizards (for summaries and references, see Roze, 1964; Broadley, 1979; McDiarmid and McCleary, 1993). Conversely, *Hypsiglena torquata*, a small North American colubrid with enlarged but ungrooved rear fangs, eats primarily lizards (>50% of prey items) but also consumes a high proportion (23%) of squa-

mate eggs (Rodríguez-Robles et al., 1999). The posterior maxillary teeth of snakes that primarily eat reptile eggs are usually laterally compressed and often described as lancet shaped, lanceolate, or bladelike (e.g., Tweedie, 1953; Roze, 1964; Broadley, 1980). These teeth are apparently used to slit the egg shells during ingestion (Roze, 1964).

Harry W. Greene (in litt.) informed me that some observations indicate that reptile eggs may be difficult for snakes to digest without first slitting the shells. Prompted by this idea, I reexamined the three remaining intact eggs removed from *P. oblectator* and, indeed, all three have one or two small slits in them that were undoubtedly made by the snake. Thus, the posterior fangs in some *Pseudoxyrhopus* (and perhaps other members of the *Pseudoxyrhopus* group) may play a more important role in egg predation (if this is frequent) than in subduing active prey. Enlarged posterior fangs are not critical adjuncts to hinged teeth in predation on hardbodied lizards, as is clearly shown by the fact that all other colubrids with hinged teeth have nonenlarged or only slightly enlarged rear teeth. Interestingly, the African hinge-toothed snake *Chamaelycus fasciatus* is also known to eat both lizard eggs and gerrhosaurids (see footnote 4). However, in this species the posterior maxillary teeth are not enlarged, whereas one or two teeth in the middle of the maxilla are enlarged and followed by a broad diastema (Parker, 1933; personal observations).

Raxworthy and Nussbaum (1994) speculated that three species of *Pseudoxyrhopus* (*P. heterurus*, *P. microps*, and *P. tritaeniatus*) might feed upon stream dwelling frogs of the genus *Mantidactylus* (Ranidae). This inference, based solely on the frequent occurrence of these snakes near streams, is unfounded; snake diets are not easily inferred from macrohabitat associations alone. *Pseudoxyrhopus tritaeniatus*, at least, is frequently found well away from streams (personal observations) and, based

on a single observation, adults feed on mammals. Neither dietary data nor morphological characters suggest that any species of *Pseudoxyrhopus* feed upon frogs.

Although it might be assumed that speculations about snake diets, such as frogs in the diet of *Pseudoxyrhopus*, are harmless, they can thwart attempts to understand the evolution of prey preferences and behavior. Such speculations tend to be picked up in the literature and become repeated so that they take on an aura of truth, despite the weak basis for the original statement. In the case of *Pseudoxyrhopus* diets, Raxworthy and Nussbaum's (1994) original speculation has already been applied to another species of *Pseudoxyrhopus*: "most likely it [*Liopholidophis infrasignatus*] is the main predator (together with *L. epistibes*, *L. rhadinacea* and *Pseudoxyrhopus sokosoko*) of many *Mantidactylus* species" (Andreone and Randriamahazo, 1997: 120). Andreone and Randriamahazo's inference was not based on new data but apparently on the assumption that Raxworthy and Nussbaum's original statement applied to other species of *Pseudoxyrhopus*; this assumption itself may or may not be a reasonable one because dietary preferences can show interspecific or geographic variation.

Moreover, Andreone and Randriamahazo (1997) provided no data to support their statement that *Liopholidophis infrasignatus*, *L. epistibes*, and *L. rhadinacea* are "most likely the main predators" of *Mantidactylus* species. The only documented prey records for these snakes are microhylid frogs (*Plethodontohyla* and *Platypelis* spp.) or their eggs in the diets of all three species and a small chamaeleon (*Chamaeleo nasutus*) in *L. infrasignatus* (Cadle, 1996a). Of the other species of *Liopholidophis*, Cadle (1996a) found only one *Mantidactylus* (in *L. lateralis*), whereas other nonmicrohylid dietary records were *Boophis* (Rhacophoridae), *Ptychadena* (Ranidae), and *Heterixalus* (Hyperoliidae). All of these dietary records are from the Ranomafana National Park, where *Manti-*

dactylus species are abundant. The prevalence of microhylids in diets of most species of *Liopholidophis* for which documentation exists (Cadle, 1996a) is highly interesting from both evolutionary and ecological viewpoints. It invites comparative analyses of snake behaviors, foraging strategies, seasonal dietary variation, and chemosensory capabilities and perhaps even of the defensive mechanisms of Malagasy frogs. Unfounded assumptions about the dietary habits of these snakes misdirect and mislead efforts to understand these interesting natural history phenomena.

Unfounded speculations about snake diets are frequent in the literature, but the determinants of snake dietary preferences are poorly understood. Diet is clearly related only in a very loose and unpredictable way to habitat preferences and prey abundance (Cadle and Greene, 1993). Progress in understanding those determinants will come from more conscientious attention to good natural history observations and knowing when speculations can be reliably extended beyond the hard facts. This attention entails, in the present case, the realization that snake diets and macrohabitats are connected only in the loosest possible way and that reliable dietary inferences cannot be made on that basis alone.

My speculation on the diets of *Pseudoxyrhopus* are rooted in known dietary variation for these species and on morphological attributes known to be associated in colubrids with particular dietary spectra. The presence of a diastema in the dentary tooth row in at least five species of *Pseudoxyrhopus* (including *P. tritaeniatus*, *P. kely*, and *P. microps*; Table 2), the presence of hinged teeth in most species of *Pseudoxyrhopus*, and the enlarged median series of dentary teeth are characters often associated in snakes with a diet of hard-bodied lizards such as skinks and gerrhosaurids (Savitzky, 1983; Greene, 1989a; see also footnote 4). These morphological characters strongly suggest that these lizards are common prey for species of *Pseu-*

doxyrhopus. Unless contradictory observations are forthcoming, the dentitional morphology and definite diet records make it unlikely that any species of *Pseudoxyrhopus* feed on frogs, contrary to Raxworthy and Nussbaum (1994) and Andreone and Randriamahazo (1997).

These inferences concerning diet would seem to be contradicted by the observation of mammal remains in the gut of an adult *Pseudoxyrhopus tritaeniatus*. However, this snake is one of three large species of *Pseudoxyrhopus* (adult SVLs > 800 mm; the other species attaining this size are *P. ankafinaensis* and *P. microps*). A common ontogenetic dietary shift seen in many species of colubrids is from a juvenile diet of lizards to an adult diet of mammals (e.g., Greene, 1989b), but it occurs only in those species attaining large body size or having special means of dealing with mammalian prey (for discussion, see Cadle and Greene, 1993). The shift seems to occur most often around a body size of 500 mm SVL (unpublished observations; also, see Greene, 1989b, fig. 1), although other factors such as body mass, venom capability, and/or constricting ability are also important (venoms and constriction are unknown in *Pseudoxyrhopus*). Accordingly, only the three large species of *Pseudoxyrhopus* routinely attain sufficient size and may show this dietary shift, although exceptionally large individuals of *P. heterurus* attain just over 500 mm SVL (Raxworthy and Nussbaum, 1994) and may also fit the pattern. Other species of *Pseudoxyrhopus* are smaller.

Intriguingly, the switch from hinged juvenile teeth in *P. tritaeniatus* to firmly ankylosed adult teeth may correlate with the suggested ontogenetic dietary shift; firmly ankylosed teeth would probably be critical in subduing struggling mammalian prey. Unfortunately, sample sizes are far too small to confirm this suspected ontogenetic shift or to examine other parameters relevant to the natural history of *Pseudoxyrhopus*, such as frequency of prey use and predator/prey mass ratios (Greene, 1983,

1989b). If confirmed, a shift from hinged to firmly ankylosed teeth in *P. tritaeniatus* correlated with an ontogenetic dietary shift would be the first instance in colubrids in which a dietary change entails a concomitant change in a specific morphological character associated with prey acquisition.

The configuration of the maxillary and dentary dentition in *Pseudoxyrhopus* is probably associated with a fundamental dietary repertoire of skinks and gerrhosaurids. However, some inter- and intraspecific variation in dental characters does occur, such as the interspecific differences in overall tooth form. Other types of dental variation occur in the related taxa *Heteroliodon*, *Pararhadinaea melanogaster*, and "*Pararhadinaea*" *albignaci*. The existence of such variation among species that share fundamental and unusual dental characteristics might imply differing degrees of morphological specialization or perhaps different prey types or dietary spectra. Based on a single observation for *Pseudoxyrhopus oblectator*, the biological role of the posterior fangs of these snakes may be associated with predation on reptile eggs rather than on active prey, although a role in both behaviors is possible (knowledge of venoms would aid in interpreting this character). The enlarged dentary teeth and the dentary diastema (possibly variable in *Pseudoxyrhopus oblectator*) appear universally among species of *Pseudoxyrhopus*. Hinged teeth are also present universally in the species examined, but the ontogenetic trend to fully ankylosed teeth observed in *P. tritaeniatus* may be characteristic of those species attaining large body sizes and perhaps switching to different (mammalian) prey.

Similar interspecific variation has been reported for some other colubrid genera. For example, Savitzky (1981) reported variation in tooth form, extent of fang enlargement, and degree of tooth hinging among species of *Liophidium*. This example is germane to the present discussion because *Liophidium* shares several unusu-

al dental characters with *Pseudoxyrhopus*, *Heteroliodon*, *Pararhadinaea melanogaster*, and "Pararhadinaea" *albignaci*. *Liophidium*, in addition, is also known to prey largely, if not exclusively, upon skinks and gerrhosaurids (Savitzky, 1981).⁷ Because all recorded activity patterns for species of *Pseudoxyrhopus* suggest exclusive nocturnality (Raxworthy and Nussbaum, 1994; personal observations), whereas potential skink and gerrhosaurid prey are all diurnal, *Pseudoxyrhopus* probably forages differently than do species of *Liophidium*, which are also diurnal (personal observations). This assumes, of course, that skinks and gerrhosaurids are the primary prey of *Pseudoxyrhopus*, which seems likely based on known diets and morphological variation.

DENTITION OF PARARHADINAEAE MELANOGASTER BOETTGER

Background

Based on new data and clarifications presented herein I reconsider the relationships of *Pseudoxyrhopus* and offer an alternative to the hypothesis presented by Raxworthy and Nussbaum (1994). However, published descriptions of dentitional characters for the other Malagasy genera presumed to be close relatives of *Pseudoxyrhopus*, *Pararhadinaea* and *Heteroliodon*, need to be corrected and augmented. *Pararhadinaea* currently has three named forms: *Pararhadinaea melanogaster* Boettger (1898) (type species),

P. albignaci Domergue (1984), and *P. melanogaster marojejyensis* Domergue (1984). *Heteroliodon* is monotypic: *Heteroliodon occipitalis* (Boulenger, 1896).

Pararhadinaea, *Heteroliodon*, and *Pseudoxyrhopus* historically have been distinguished in part on the basis of maxillary and dentary dentition (e.g., Guibé, 1958; Raxworthy and Nussbaum, 1994). For example, the absence of a maxillary diastema in *Pararhadinaea* was used to distinguish that genus, known at the time only from *P. melanogaster* Boettger, from *Pseudoxyrhopus* (Guibé, 1958). However, this character varies within *Pseudoxyrhopus*. More importantly, the maxillary and dentary dentitions of "Pararhadinaea" *albignaci* and of *Pararhadinaea melanogaster* are morphologically very dissimilar. The dentition of neither species has been accurately described apart from Boettger's (1898) incomplete description for *P. melanogaster*. Thus, despite the strong differences between these species, some dentitional characters of "Pararhadinaea" *albignaci* have been assumed to apply to *P. melanogaster* (type species of *Pararhadinaea*) and have been used in diagnoses and descriptions of *Pararhadinaea* (Raxworthy and Nussbaum, 1994). In addition, "Pararhadinaea" *albignaci* has a dentition that is unique among the genera under consideration (and unusual among colubrids generally); no one has previously called attention to these unique characteristics. The confusion has resulted in the erroneous attribution of some characters to *Pararhadinaea* and failure to appreciate dentitional diversity in these snakes. Similarly, Raxworthy and Nussbaum (1994) inaccurately described the dentition of *Heteroliodon* and failed to note some of its unusual characters.

Because proper attribution of characters and accurate descriptions are germane to the phylogenetic hypotheses for these snakes, I first unravel the confusion created by the most recent review (Raxworthy and Nussbaum, 1994) and then augment previously published descriptions. Because

⁷ To Savitzky's (1981) data can be added the following. The stomach of MCZ 180381 (*Liophidium rhodogaster*; SVL 169 mm, 2 g in life) contained two pieces of broken tail from the skink *Anphiglossus melanopleura*. The tail pieces showed essentially no evidence of digestion, indicating recent ingestion; the snake was captured at 1345 h and thus was foraging during the day. Most likely, the skink was grabbed by the tail and escaped, leaving the snake with the autotomized portions of the tail. A specimen of *Liophidium torquatum* (BMNH 89.4.11.10.15; SVL 454 mm, 52 g preserved) contained in its stomach an intact *Zonosaurus madagascariensis* (Gerrhosauridae) (SVL 47 mm, 2.5 g preserved), swallowed tail first.

the dental differences between *Pararhadinaca melanogaster* Boettger (type species) and "*Pararhadinaca*" *albignaci* Domergue bear on proper diagnosis of *Pararhadinaca* and on the generic allocation of "*Pararhadinaca*" *albignaci*, I begin with a redescription of the dentition of the holotype of *P. melanogaster*. Descriptions of the dentition of "*Pararhadinaca*" *albignaci* and *Heterohodon occipitalis* follow.

Redescription of the Dentition of *Pararhadinaca melanogaster* Boettger (Fig. 7)

Boettger's (1898: 33) description of the dentition of the holotype of *Pararhadinaca melanogaster* (SMF 17885) is essentially correct (my translation):

—Upper jaw [Maxilla] delicate and slender, with about 17 delicate, equally spaced teeth that gradually increase in length toward the back, only the rear-most measurably enlarged, compressed. Lower jaw broad, robust, with 11 rather blunt teeth, the anterior [ones] small, gradually becoming larger toward the back; from the sixth considerably larger and broadly supported.

Additional details reported here are based on my study of the holotype (Fig. 7). Both maxillae (+anterior tip of each ectopterygoid) and the right dentary (+anterior tip of compound bone) had been previously dissected from the specimen, probably by Boettger, and are in an associated vial.

Maxillary teeth 14+2 (left) and 13+2 (right), the last two teeth enlarged and ungrooved (inferred from the tooth socket size and the posterior fang on the left side, which although loose is the only fang still in place). No diastema separating the fangs from the anterior teeth. Anterior maxillary teeth gradually increase in size anterior to posterior, and the most posterior tooth of this series is only slightly smaller than the fangs (Fig. 7).

Dentary teeth 12, gradually increasing in size from the first to the sixth. Teeth 7–10 are larger and more robust than the anterior series and are approximately the same size as one another. Tooth 11 is mis-

sing but judging from the socket it was slightly smaller than tooth 10. Tooth 12 is much smaller than teeth 7–10. An unusual feature is the exceptionally wide spaces between teeth 7–10 (Fig. 7). The lower jaw itself is also robust, particularly considering the size of this snake (239 mm total length).

Aside from a minor difference in tooth counts and the few additional details noted here, my assessment of the dentition of *Pararhadinaca melanogaster* is similar to that of Boettger (1898). Boettger noted that the dentary teeth of *P. melanogaster* were "rather blunt." In fact, both maxillary and dentary teeth are somewhat blunt and robust. The maxillary teeth (except for the fangs) and the anterior dentary teeth are slightly compressed anteroposteriorly at their tips and are hinged; they can be deflected with a fine needle. Most tooth sockets are occupied by functional teeth, which suggests that alternate tooth replacement has been modified. Following Boettger (1898), Mocquard (1909: 41) and Guibé (1958) correctly described the general configuration of the maxillary and dentary dentition of *P. melanogaster*, but subsequent accounts have erred in essential details.

The dentary dentition of *Pararhadinaca melanogaster* is different than the characterization of *Pararhadinaca* given by Raxworthy and Nussbaum (1994: 30): "anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged" (cf. Fig. 7). The error is based on their examination of "*Pararhadinaca*" *albignaci*, which does have a pair of median enlarged dentary teeth similar to those of *Pseudoxyrhopus* (but different from those of *Pararhadinaca melanogaster*; Fig. 7), and a mistranslation of Boettger's (1898) description of the dentary teeth of *Pararhadinaca melanogaster*: Raxworthy and Nussbaum's (1994: 32) translation ("11 dentary teeth, the sixth considerably enlarged") missed a small but crucial part of Boettger's description (which was correctly quoted by Mocquard

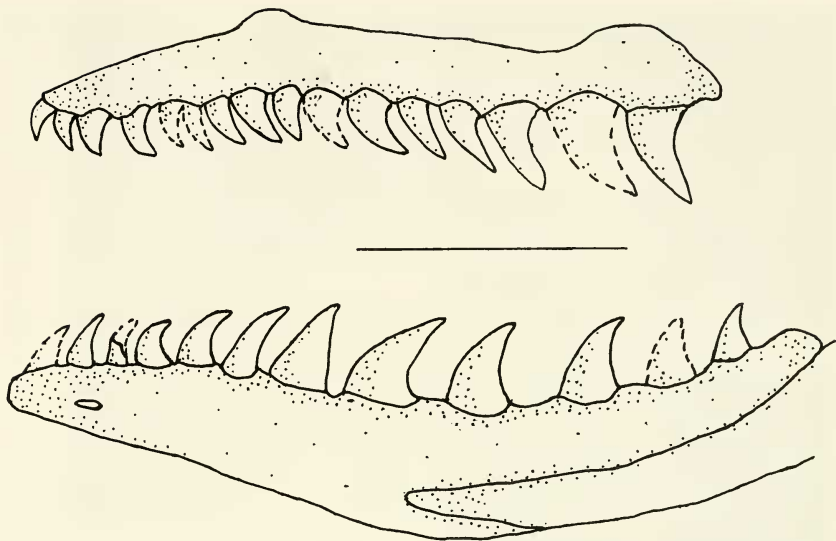


Figure 7. Left maxilla and right dentary (reversed) of *Pararhadinaea melanogaster* Boettger (holotype, SMF 17885). Teeth drawn with dotted lines are missing. As in *Pseudoxyrhopus oblectator* (see Fig. 4), some of the teeth in this specimen were detached anterobasally and folded down; these have been restored to their normal position in the drawing. Scale bar = 1 mm.

[1909] and Guibé [1958]): “11 . . . teeth . . . gradually becoming larger toward the back; from the sixth [vom sechsten] considerably larger” (emphasis added). Thus, *Pararhadinaea melanogaster* does not have one or two enlarged dentary teeth, but the entire posterior series after the sixth tooth (except the last tooth) is greatly enlarged (Fig. 7). Apart from mischaracterizing the dentary dentition of *Pararhadinaea melanogaster*, Raxworthy and Nussbaum (1994) overlooked critical aspects of the maxillary dentition of “*Pararhadinaea*” *albignaci*.

The interpretation of *Pararhadinaea* as having “one or two enlarged median dentary teeth” is problematic because all dentary teeth posterior to the first five or six are enlarged (Fig. 7). One interpretation of this condition is that *Pararhadinaea* has enlarged median dentary teeth (a character homologous with that of *Pseudoxyrhopus*, “*Pararhadinaea*” *albignaci*, and

Heteroliodon) and enlarged posterior dentary teeth. However, the wide spacing of the posterior dentary teeth in *Pararhadinaea melanogaster* is quite different from and possibly not homologous with the condition in the other taxa. This ambiguity has important consequences for understanding the relationships of *Pararhadinaea*.

Aside from the holotype of *Pararhadinaea melanogaster* (Fig. 8), the species is known definitely from only two other specimens, the holotypes of *P. m. marojejyensis* Domergue, 1984 (MNH 1982-1220; Fig. 9) and *Rhabdotophis subcaudalis* Werner, 1909 (SMNS 4235; see Schlüter and Hallermann, 1997). Boettger (1913: 326) stated that another specimen was in the Naturhistorische Museums in Lübeck, Germany, but its present status is unknown.

The dentitions of the holotypes of *Pararhadinaea m. marojejyensis* and *Rhabdo-*

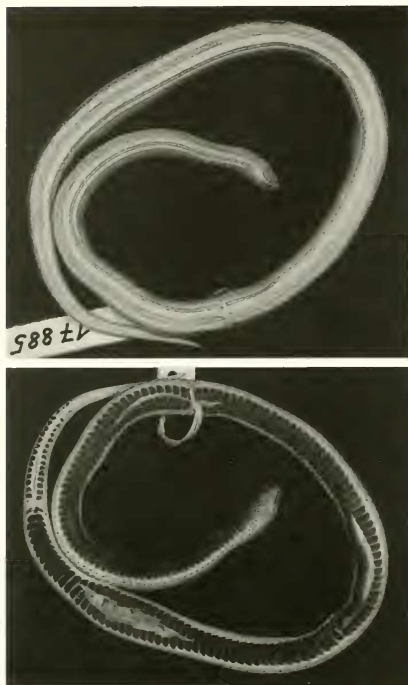


Figure 8. Dorsal and ventral views of the holotype of *Pararhadinaea melanogaster* Boettger (SMF 17885). Total length = 239 mm. Approximately $\times 1.08$.

trophis subcaudalis are identical in configuration to that of the type of *P. melanogaster*. MNHN 1982-1220 and SMNS 4235 have, respectively, 12+2 and 14+2 maxillary teeth on the right side (the left maxilla of SMNS 4235 is missing). As in SMF 17885 the maxillary teeth in both specimens gradually increase in size posteriorly, a diastema is absent, and the fangs are ungrooved and slightly larger than the immediately preceding teeth. In both MNHN 1982-1220 and SMNS 4235 the tooth immediately preceding the first fang is approximately two-thirds the length of the fangs (three quarters of the length in SMF 17885). All maxillary teeth are

hinged except for the fangs (and perhaps the last tooth immediately preceding the fangs in MNHN 1982-1220).

SMNS 4235 has 14 dentary teeth on each side. The anterior dentary teeth are small and hinged. Teeth 7-9 are abruptly enlarged (especially teeth 8 and 9), and these are followed by five large, widely spaced teeth similar to those of SMF 17885 (Fig. 7); narrow gaps separate the first nine dentary teeth. Apart from the first six teeth, none of the dentary teeth are hinged. In MNHN 1982-1220 the anterior six dentary teeth are small and hinged, and these are followed by five or more enlarged, firmly ankylosed, widely spaced teeth (the posterior dentary teeth of this specimen were not thoroughly investigated).

A Comparison of the Known Specimens of *Pararhadinaea melanogaster* Boettger

The three known specimens of *Pararhadinaea melanogaster* have never been directly compared and some comment on their characters seems warranted. The provenance of the type of *Rhabdotophis subcaudalis* is unspecific (type locality: "Madagascar"), whereas the other two specimens are from two widely separated localities in northern Madagascar: Nosy Be, an island off the northwest coast (type of *P. melanogaster*) and the Marojejy region of northeastern Madagascar (type of *P. m. marojejyensis*). Domergue's (1984: 152) statement of the type locality for *P. m. marojejyensis* ("Forêt du massif montagneux du Marojejy") implies that the snake was collected in the high mountains of the Marojejy region, which attain elevations greater than 2,000 m; this has been the interpretation of other authors (e.g., Glaw and Vences, 1994). However, Charles P. Blanc, who collected the specimen during a survey of the Marojejy region in the early 1970s, informed me that the snake was collected near sea level on the coast. Thus, it was probably collected outside the present limits of the Reserve Naturelle Integrale de Marojejy, whose

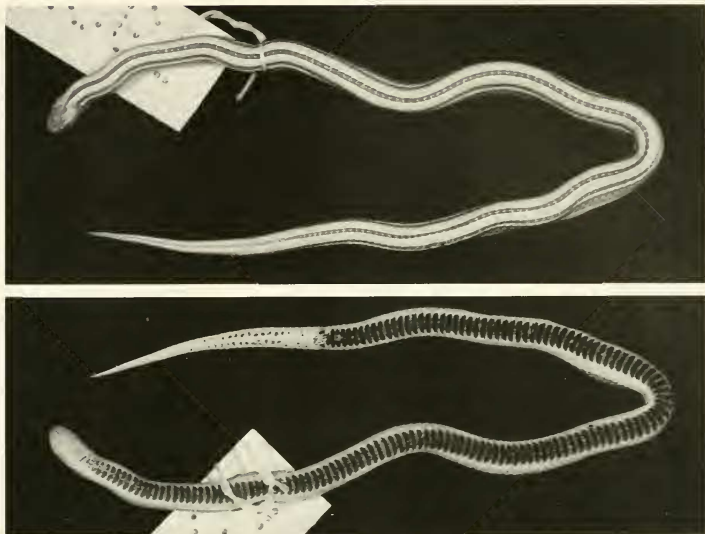


Figure 9. Dorsal and ventral views of the holotype of *Pararhadinaea melanogaster marojejensis* Domergue (MNHN 1982-1220). Total length = 185 mm. Approximately $\times 1.14$.

eastern boundary lies some 40 km from the coast (Nicoll and Langrand, 1989). (For additional details about the circumstances of capture of this specimen, see the later discussion of character 11.)

A summary of standard systematic characters for the three specimens of *Pararhadinaea melanogaster* is given in Table 3. Apart from a markedly lower ventral scale count in MNHN 1982-1220, all characters are essentially the same in the three specimens. The low ventral scale count of MNHN 1982-1220 as compared with the type of *P. melanogaster* was Domergue's (1984) primary reason for naming that specimen as a subspecies of *P. melanogaster*; however, in the absence of knowledge of populational variation the distinction seems pointless.

The three specimens differ somewhat in color pattern (colors in life are unknown). MNHN 1982-1220 and SMNS 4235 have more irregular markings than does SMF

17885, and the width of the stripes varies among the specimens. In SMF 17885 the stripes are centered at midbody on row 3 (plus half of the adjacent rows), on the suture between rows 5 and 6 (covering half of each row), and on row 9 (plus half of the adjacent rows). In MNHN 1982-1220 the lateral stripe is slightly broader (row 3 + two-thirds of the adjacent rows) and the vertebral stripe is slightly narrower (row 9 + one-third of the adjacent rows). In SMNS 4235 the lateral stripe is still broader (rows 2 and 3 + lower half of row 4 and upper edge of row 1), whereas the dorso-lateral and vertebral stripes are about the same as in MNHN 1982-1220. Additionally, in SMNH 4235 dorsal row 1 is heavily and irregularly speckled with dark pigment, making the lateral stripe appear even broader.

The proper taxonomic allocation of *Rhabdotophis subcaudalis* has been in dispute. After describing *R. subcaudalis* in

TABLE 3. SCALE COUNTS, MEASUREMENTS, AND OTHER DATA FOR THE THREE KNOWN SPECIMENS OF *PARARHADINAEA MELANOGASTER* BOETTGER. BILATERAL COUNTS (E.G., HEAD SCALES AND POSTERIOR SCALE REDUCTION) ARE GIVEN FIRST FOR THE LEFT SIDE, THEN FOR THE RIGHT.

	SMF 17855 (holotype)	MNHN 1982-1220 (holotype of <i>P. n. marojejensis</i> Domergue (1984))	SMNS 4235 (holotype of <i>Rhabdotophis subcaudalis</i> Werner (1909))
Sex	female	female	male
Total length (SVL ¹) (mm)	239 (201)	185 (152)	212 (182)
Tail length (mm)	38	33	30
Tail length/total length	0.16	0.18	0.14
Maxillary teeth	14+2 13+2	12+2	14+2
Dorsal scales	17-17-17	17-17-17	17-17-17
Ventral scales	163	145	168
Subcaudal scales	40	41	37
Anal scale	divided	divided	divided
Preocular scales	1, 1	1, 1	1, 1
Postocular scales	2, 2	2, 2	2, 2
Temporal scales			
Anterior	1, 1	1, 1	1, 1
Posterior	2, 2	2, 2	2, 2
Supralabial scales (touching eye)	7, 7 (3+4)	7, 7 (3+4)	7, 7 (3+4)
Infralabial scales	8, ?	8, 9	8, 8

¹SVL = snout-vent length.

1909, Werner synonymized it with *Pararhadinaea melanogaster* Boettger (Werner, 1929). The synonymy did not originate with Guibé (1958), as thought by Brygoo (1983) and Raxworthy and Nussbaum (1994), who nevertheless followed Werner and Guibé in this regard. However, Boulenger (1915) synonymized *Rhabdotophis* with *Pseudoxyrhopus* and recognized *subcaudalis* as a valid species of *Pseudoxyrhopus*, at the same time maintaining the validity of *Pararhadinaea melanogaster*. My comparison of the types of *R. subcaudalis* and *P. melanogaster* conclusively show that both names refer to the same taxon, *Pararhadinaea melanogaster*.

Several characteristics of *Rhabdotophis subcaudalis*, as described by Werner (1909), are not quite accurate and may account for some of the confusion about the proper allocation of the name. For example, Werner (1909: 58) described (in part) the dentition and color pattern of *Rhabdotophis* as follows (my translation):

—Upper jaw [maxillary] teeth gradually increasing

in size from front to back (about 10–12), the last very robust, conical, and slightly curved, not separated from the preceding by an interspace. The front lower jaw [dentary] teeth somewhat elongated. . . . A dark postocular stripe running along the flanks in a longitudinal band over 3½ scales wide.

As indicated in the descriptions of dentition for *Pararhadinaea melanogaster*, Werner (1909) miscounted the maxillary teeth (SMNS 4235 has 16 total maxillary teeth), and rather than having somewhat elongated anterior dentary teeth, the dentary teeth of SMNS 4235 are like those of *P. melanogaster*, in which the anterior six dentary teeth are actually smaller than any other teeth in the lower jaw. Werner's description of the anterior dentary teeth of *R. subcaudalis* as "somewhat elongated" implies that they were longer than more posterior teeth, a condition that more closely approximates the condition in some species of *Pseudoxyrhopus* (see Fig. 6). This may be the reason Boulenger (1915) synonymized the two genera. Additionally, although the lateral stripe in SMNS 4235 is broader than that in the other two spec-

imens (but not fully 3.5 scales wide), all three specimens of *P. melanogaster* differ from one another in the width of the stripes.

DENTITION OF "PARARHADINAEA" *ALBIGNACI* DOMERGUE AND A NEW GENUS

Subsequent to Guibé's (1958) review, Domergue (1984) described two new forms of *Pararhadinaea*, *P. melanogaster marojejensis* and "*Pararhadinaea*" *albignaci*. Although Domergue did not examine the dentition of *P. m. marojejensis*, it is similar to that of the nominal form. However, Domergue (1984: 153) described the maxillary dentition of "*Pararhadinaea*" *albignaci* as follows (my translation): "5 small anterior teeth, subequal, separated by a long interval from a single tooth that appears somewhat more robust." In reviewing the systematics of *Pararhadinaea*, Raxworthy and Nussbaum (1994) only studied material of "*Pararhadinaea*" *albignaci*, relying on Boettger's and Domergue's descriptions for the other forms. Unfortunately, both the maxillary and dentary dentitions of "*Pararhadinaea*" *albignaci* are substantially different from those of *P. melanogaster*, type species of *Pararhadinaea*. Moreover, Domergue (1984) and Raxworthy and Nussbaum (1994) failed to notice some highly unusual features of the dentition of "*Pararhadinaea*" *albignaci*. These omissions resulted in an erroneous characterization of both the maxillary and dentary dentition of *Pararhadinaea* (see above discussion of *P. melanogaster*) (Raxworthy and Nussbaum, 1994: 29–30):

posteriormost one or two teeth of maxilla enlarged compared to anterior teeth; anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged . . . [the enlarged posterior maxillary teeth] may be separated from the anterior teeth by a diastema.

The dentition of *Pararhadinaea melanogaster* differs from Raxworthy and Nussbaum's (1994) description in several ways. First, reference to a single fang in *Pararhadinaea* undoubtedly resulted from fail-

ure to observe empty tooth sockets. The three known specimens of *P. melanogaster* and two specimens of "*Pararhadinaea*" *albignaci* I examined have two fangs and/or sockets. Second, although the rear maxillary teeth of *P. melanogaster* are enlarged, they are only marginally enlarged over the next anterior teeth (Fig. 7). This condition differs from that in "*Pararhadinaea*" *albignaci*, in which the rear fangs are massively enlarged. Third, *P. melanogaster* lacks a maxillary diastema (an exceptionally broad one is present in "*Pararhadinaea*" *albignaci*). Fourth, in *P. melanogaster* the posterior dentary teeth are much more massive than the anterior dentary teeth (Fig. 7). Fifth, *P. melanogaster* lacks an enlarged median or anterior series of dentary teeth; instead, approximately the posterior half of the dentary series is enlarged (Fig. 7). However, "*Pararhadinaea*" *albignaci* does have an enlarged median series of dentary teeth.

All previous descriptions of dentition in *Pararhadinaea*, including Boettger's (1898) for *P. melanogaster*, suggest a rather common colubrid maxillary dentition: a series of small, equally spaced teeth that gradually increase in size posteriorly followed by a pair of slightly enlarged fangs. Aside from the shape of the teeth, the maxillary dentition of *P. melanogaster* conforms to this common pattern (Fig. 7). Interspecific variation in the maxillary diastema is suggested by Boettger's characterization of *P. melanogaster* (diastema absent) compared with the descriptions by Domergue and Raxworthy and Nussbaum (1994) for "*Pararhadinaea*" *albignaci* (diastema present). This is, in fact, the case (Figs. 7, 10), but there is much more. The only hint of an unusual feature is Domergue's (1984) vague indication of a "long interval" separating the fang of "*Pararhadinaea*" *albignaci* from the five anterior teeth. However, Domergue (1984: 156) thought the teeth were simply missing from the interval (rather than the space being edentulous) because the specimen was a roadkill and he thought it had perhaps deteriorated. In

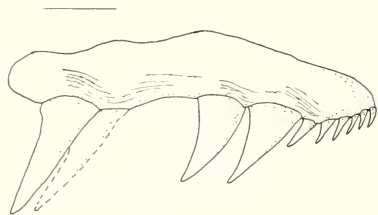


Figure 10. Right maxilla of "*Pararhadinaea*" *albignaci* (UMMZ 203642) showing the unusual enlarged teeth in the middle of the maxilla followed by an extremely broad diastema. The specimen was drawn from the fluid specimen in situ. Hence, the upper edge of the maxilla as drawn reflects only the soft tissue of the upper jaw and not the dorsal edge of the maxilla. The figure does not adequately portray the strong flexure about the enlarged median teeth, nor the nearly transverse placement of the sockets for the rear fangs (see text). This species is transferred to the new genus *Exallodontophis* herein. Scale bar = 1 mm.

fact, the maxillary and dentary dentition of "*Pararhadinaea*" *albignaci* Domergue is dramatically different from that of *P. melanogaster*.

I examined the dentition of two specimens of "*Pararhadinaea*" *albignaci*: MNHN 1982-1221 (holotype) and UMMZ 203642. In the maxilla (Fig. 10) a short anterior series of small teeth is followed by a pair of greatly enlarged teeth (still on the anterior half of the maxilla). A broad diastema and a pair of enlarged, ungrooved rear fangs follow the anterior series. The maxilla itself is rather short and strongly flexed about the point of the enlarged median teeth. Anterior and posterior to this point the maxilla curves strongly medially. The anterior fang on the right side of UMMZ 203642 is missing, but another unusual feature is the nearly transverse alignment of the sockets for the posterior fangs. The posterior fang is strongly offset laterad from the anterior fang. On the left side of this specimen, the two rear fangs are in place and their bases strongly overlap when viewed from the side.

The morphology and dentition of "*Pararhadinaea*" *albignaci* is highly unusual in having (1) two greatly enlarged teeth at the end of the anterior series of teeth, i.e., in the middle of the maxilla, (2) an excep-

tionally broad diastema between these enlarged teeth and the ungrooved fangs, and (3) a strong flexure in the middle of the maxilla. In addition, the small teeth anterior to the median enlarged teeth are hinged in the UMMZ specimen of "*Pararhadinaea*" *albignaci* (I was unaware of the hinged teeth in these snakes in 1994 when I examined the type of "*Pararhadinaea*" *albignaci* and hence did not check for it). The dentition of "*Pararhadinaea*" *albignaci* (UMMZ 203642; Fig. 10) is typical: 8+2 maxillary teeth. Teeth 1-6 are small, somewhat kinetic, and gradually increase in size. Teeth 7 and 8 are massively enlarged and akinetic; these enlarged teeth are positioned at a level slightly anterior to the eye underneath the third supralabial and just anterior to the approximate midpoint of the maxilla. The diastema between the eighth tooth and the first fang is equivalent to about one-third the length of the maxillary tooth row, i.e., from the anterior tooth to the anterior edge of the first fang. All teeth in "*Pararhadinaea*" *albignaci*, including the small anterior series, are rather stout and bluntly pointed. In addition, the enlarged teeth are proportionally much larger in relation to the overall size of the maxilla and other maxillary teeth than is typical for colubrids (cf. Fig. 10 and Figs. 6, 7, 12, 16). The maxillary dentition of the holotype is morphologically similar to that of UMMZ 203642 except that only six teeth are present anterior to the diastema (as reported also for UMMZ 200064 by Raxworthy and Nussbaum, 1994).

The dentary dentition of "*Pararhadinaea*" *albignaci* (UMMZ 203642) consists of a series of four small anterior teeth that gradually increase in size, a somewhat abruptly enlarged fifth tooth, and two massively enlarged teeth (teeth 6 and 7). The enlarged teeth are followed by a short diastema (approximately equivalent to or slightly less than the base of the following tooth). Because thorough study of the posterior dentary dentition requires destructive manipulation of specimens I did not

examine the posterior dentary dentition further. The first three anterior dentary teeth are smaller than the posterior teeth, whereas the fourth and fifth are subequal to the posterior teeth.

The maxilla and maxillary dentition of "*Pararhadinaea*" *albignaci* differ from those of *P. melanogaster* (cf. Figs. 7 and 10) in having (1) fewer teeth (6-8+2 vs. 12-14+2), (2) a pair of greatly enlarged teeth in the middle of the maxillary tooth row (absent in *P. melanogaster*), (3) an exceptionally broad diastema between the median enlarged teeth and the posterior fangs (absent in *P. melanogaster*), and (4) a shortened, robust, and strongly flexed maxilla (longer, gracile, and relatively straight in *P. melanogaster*). The maxillary dentition of "*Pararhadinaea*" *albignaci* is also very different from that of *Pseudoxyrhopus* (Fig. 6) and *Heteroliodon* (Fig. 12), but *Pseudoxyrhopus* and "*Pararhadinaea*" *albignaci* have a dentary diastema, an unusual character for colubrids.

The strong divergence in maxillary dentition between "*Pararhadinaea*" *albignaci* and *P. melanogaster* requires reconsideration of the attribution of *albignaci* to *Pararhadinaea*. Domergue (1984) did not fully justify his generic placement, noting only a few characters of habitus and scallation in his redefinition of *Pararhadinaea* (Domergue, 1984: 155-156). He was perhaps influenced by the fact that "*Pararhadinaea*" *albignaci* and *P. melanogaster* have black venters (see Figs. 8, 9, 11), a somewhat uncommon character in colubrids. In fact, most of the defining characters given by Domergue (e.g., small size, short head little distinct from the neck, short tail, small eye) typify many small cryptozoic colubrids (Cadle and Greene, 1993), including species of other genera from Madagascar. Others (hypapophyses on posterior trunk vertebrae) characterize a wide array of Afro-Malagasy colubrids. Raxworthy and Nussbaum (1994) used similar characters to diagnose *Pararhadinaea* but failed to realize the substantial divergence in dentition between "*Parar-*

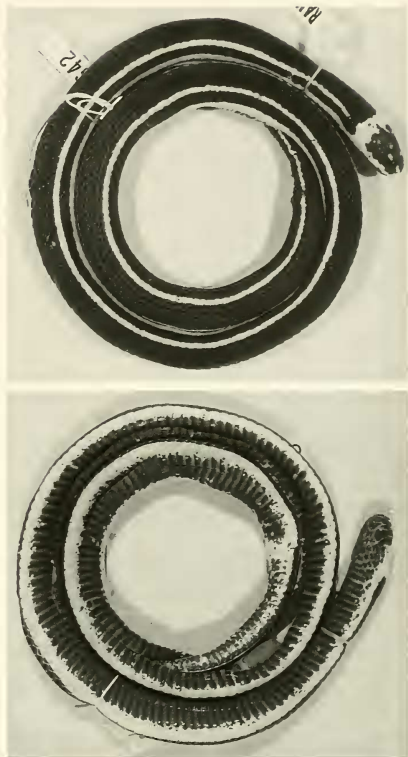


Figure 11. Dorsal and ventral views of *Exallodontophis albignaci* (UMMZ 203642). Total length = 461 mm.

hadinaea" *albignaci* and *P. melanogaster*. Thus, their diagnosis of *Pararhadinaea* included dentitional characters ("anterior dentary teeth same size as posterior dentary teeth, middle one or two dentary teeth considerably enlarged"; Raxworthy and Nussbaum, 1994: 30) that do not apply to the type species (see Fig. 7). Moreover, although Raxworthy and Nussbaum (1994) observed a maxillary diastema in "*Pararhadinaea*" *albignaci* they failed to grasp how unusual its exceptional breadth is for a colubrid and did not comment at all on the highly unusual presence of en-

larged teeth in the middle of the maxilla (Fig. 10). In essence, the three nominal taxa currently in *Pararhadinaca* have been placed together on the basis of a suite of characters shared by many small terrestrial and/or cryptozoic colubrids and an erroneous understanding of their dentition.

Because colubrid genera are generally diagnosed in part by sharing basic similarity in the configuration of the dentition (especially on the maxilla), I here transfer "*Pararhadinaca*" *albignaci* Domergue to a new genus to reflect its substantial dentitional divergence from the type species of *Pararhadinaca*, *P. melanogaster* Boettger. Of course, one procedure to maintain current nomenclature would be to broaden the diagnosis of *Pararhadinaca* to accommodate a greater diversity of both maxillary and dentary tooth configurations. However, not only would this be counter to usual procedures in colubrid systematics, but evidence adduced below suggests that "*Pararhadinaca*" *albignaci* is more closely related to *Pseudoxyrhophus* and *Heteroliodon* than to *Pararhadinaca melanogaster*. Maintaining *albignaci* in *Pararhadinaca* would thus render the genus nonmonophyletic.

No generic name is currently available to accommodate "*Pararhadinaca*" *albignaci*, for which the following new genus is proposed.

Exallodontophis
new genus

Figures 10, 11

Type Species. *Pararhadinaca albignaci* Domergue, 1984.

Etymology. From the Greek *exallos* (quite different, special, distinguished) + *odontos* (of teeth; from *odous*, tooth) + *ophis* (snake), or "snake of quite different teeth," referring to the unusual maxillary dentition. Gender masculine.

Content. A single species, *Exallodontophis albignaci* (Domergue, 1984).

Definition and Diagnosis. Based on detailed study of UMMZ 203642 and MNHN 1982.1221; augmented with vari-

ation reported for "*Pararhadinaca*" *albignaci* by Raxworthy and Nussbaum (1994). Small, slender terrestrial or cryptozoic colubrids (largest females 415 and 416 mm total length; largest male 291 mm total length). Tail short (11% of total length) and stout. Pupil round. Eye very small, 20% of head depth at midorbit. *Vertebrae:* Hypapophyses present on posterior trunk vertebrae. The hypapophyses are short and with a bluntly pointed posterior projection that barely overlaps the succeeding vertebra. *Dentition:* Maxilla with an anterior series of four to six teeth gradually increasing in size followed by two exceptionally large, ungrooved teeth, a very broad diastema, and two enlarged, ungrooved rear fangs (standard maxillary formula 6-S+2) (Fig. 10). The enlarged median maxillary teeth are immediately anterior to the approximate midpoint of the maxilla; each is about three-quarters of the length of the posterior fangs and at least twice the length and much more massive than any anterior teeth in the maxilla. Dentary with a series of about five teeth that gradually increase in size, followed by a pair of greatly enlarged teeth, a short diastema, and a series of smaller teeth. Maxillary teeth except for the enlarged ones are hinged, but the dentary teeth do not appear to be so. *Scutellation:* Ventrals 180–196. Anal divided. Low number of subcaudals (30–37).⁵ Smooth dorsal scales in 17–17–17 rows (no posterior reduction). No apical pits. Supralabials seven, with labials three and four touching the eye. Loreal absent. One small preocular. Infralabials eight. Temporals one + two. *Hemipenis:* "Spinose" (Domergue, 1984), but structural details are unknown.

These traits distinguish *Exallodontophis* from other genera of snakes. The enlarged pair of ungrooved teeth in the middle of the maxilla and the exceptionally broad maxillary diastema are characters distin-

⁵ Raxworthy and Nussbaum (1994: 31) reported 10 subcaudal scales in one specimen. This is probably an error or is based on an incomplete tail.

guishing it from all other genera of Malagasy colubrids. The external appearance and configuration of the dentary dentition of *Exallodontophis* are similar to those of *Pseudoxyrhopus*, but species of *Pseudoxyrhopus* have a loreal scale, 19 or more midbody dorsal scale rows that undergo posterior reduction, and longer tails (14–22% of total length). The maxillary and dentary dentition distinguish *Exallodontophis* from the now monotypic *Pararhadinaea*. *Mimophis* has somewhat enlarged median maxillary teeth (see Bogert, 1940, fig. 15) but lacks a broad maxillary diastema, has grooved rear fangs, and differs in habitus and scutellation from *Exallodontophis*. Some African genera referred to as aparallactines (see Underwood and Kochva, 1993) are superficially similar to *Exallodontophis* and have shortened maxillae with a pair of enlarged teeth situated approximately beneath the eye. However, in these cases the fangs are grooved and are not followed by a diastema and another pair of enlarged teeth.

Distribution. Eastern Madagascar from the vicinity of Perinet (18°56'S, 48°25'E) to Montagne d'Ambre at the northern tip of the island (12°32'S, 49°10'E) (after Raxworthy and Nussbaum, 1994, fig. 23). The three known localities are all within or adjacent to protected areas (Analamazaotra Special Reserve, Marojejy Strict Reserve, and Montagne d'Ambre National Park).

Description and Comparison of Dentition. *Exallodontophis albignaci* is known from few specimens (four were reported by Raxworthy and Nussbaum [1994], and at least one has been obtained since). Apart from the dental characters described here for the first time, standard scutellational characters and natural history were summarized by Domergue (1984) and Raxworthy and Nussbaum (1994). Although no dietary data are available for *Exallodontophis*, the configuration of the maxillary and dentary dentition suggests a diet of skinks or other hard-bodied lizard prey.

I am unaware of other colubrids with a

maxillary dentition like that of *Exallodontophis*. However, some colubrids do have enlarged maxillary teeth positioned more or less as in *Exallodontophis* with respect to, for example, the eye. Among these are many of the African genera frequently referred to as aparallactines (e.g., *Amblyodipsas*, *Aparallactus*, *Miodon*, *Macrelaps*, *Polemon*, *Xenocalamus*; see generic diagnoses and fig. 18 of Boulenger, 1896: 244–256). *Exallodontophis* differs from these genera in anatomical details. In aparallactines the enlarged teeth are grooved and are separated by a broad diastema from the preceding small teeth (cf. Fig. 10). Moreover, these enlarged teeth in aparallactines are not followed by another pair of fangs, as in *Exallodontophis*. Shortening of the maxillae seems to be correlated with burrowing habits in colubrids, as suggested by Bogert (1940: 84) among others, and both aparallactines and *Exallodontophis* are known to be at least somewhat fossorial (Broadley, 1983; Raxworthy and Nussbaum, 1994). The superficial resemblances between *Exallodontophis* and aparallactines in the form of the maxilla are possibly due to the constraints imposed by fossorial habits. However, the detailed structural differences between them suggests that *Exallodontophis* is unrelated to aparallactines. Parker (1927) discussed a similar case of putative homoplasy between aparallactines and some fossorial Neotropical colubrids (*Apostolepis* and *Elapomorphus*), which are similar to both *Exallodontophis* and (especially) aparallactines in some of the characters just mentioned (see also Underwood and Kochva, 1993).

Some other nonfossorial African colubrids have enlarged teeth in the middle of the maxilla as well as a pair of posterior fangs (e.g., *Psammophis*; see Bogert, 1940, fig. 15). As with aparallactines, the morphological details in these genera are quite distinct from those of *Exallodontophis*. In these genera the maxillae are relatively much longer than those of *Exallodontophis*, the posterior fangs (but not the median enlarged teeth) are grooved, and the

space between the median and posterior enlarged teeth is occupied by additional teeth as well as a diastema. No characters suggest a special relationship between *Exallodontophis* and these African genera.

DENTITION AND HEMIPENIS OF *HETEROIODON OCCIPITALIS* (BOULENGER)

Dentition

Boettger (1913) did not examine the dentition in his new genus *Heteroliodon*. Guibé (1958: 218) reported "10 to 15 [maxillary] teeth, the last 2 larger and separated from the preceding by a space. Mandibular teeth subequal." Raxworthy and Nussbaum (1994: 25) described the dentition of *Heteroliodon*:

without grooves on teeth; two posteriormost teeth of maxilla separated by a small diastema from anterior teeth; one or both posterior maxillary teeth slightly enlarged compared to anterior teeth; anterior dentary teeth same size as posterior dentary teeth, middle (fifth and sixth) dentary teeth considerably enlarged.

I examined the dentition of the holotype of *Heteroliodon occipitalis* (BMNH 1946.1.12.28) and another specimen (BMNH 1930.7.1.238). Some details differ from previous descriptions, and other noteworthy details have not previously been reported. Because the maxillae of BMNH 1930.7.1.238 are relatively undamaged as compared with those of the holotype, most of the description is based on this specimen.

BMNH 1930.7.1.238 has 11+2 maxillary teeth on each side (Fig. 12). No diastema separates the ungrooved fangs from the anterior teeth. The fangs are greatly enlarged (twice or slightly more) compared with the anterior teeth (not slightly enlarged, as reported by Raxworthy and Nussbaum, 1994). Each maxilla has an unusual edentulous extension (no tooth sockets) anterior to the tooth row sufficient to accommodate one or two additional teeth. By contrast, in most colubrids the maxilla is toothed up to and including the anterior

tip of the bone (see Figs. 6, 7, 10). All maxillary teeth except the fangs are hinged.

Raxworthy and Nussbaum (1994: 27) claimed that in the holotype of *Heteroliodon occipitalis* the anterior fang was "slightly larger" (left side) or the "same size" (right side) as the anterior teeth (the posterior fang is missing on each side). This asymmetry and the impression of the fangs being no more than slightly larger than the anterior teeth are artifacts: both fangs in the holotype are broken off at their tips (a greater portion broken on the right side than on the left). The intact teeth were undoubtedly much larger than the anterior teeth and symmetric, as in BMNH 1930.7.1.238 (Fig. 12). Raxworthy and Nussbaum (1994: 26) also reported that in UMMZ 197143 the fangs were enlarged "only very slightly," but I suspect either damaged teeth or an erroneous interpretation based on the above observations. The maxillary tooth formulae of the holotype of *Heteroliodon occipitalis* are 10+2 (left) and 11+2 (right). The fangs are greatly enlarged (as in Fig. 12) and separated from the anterior teeth by a space less than one tooth in width (but greater than the gap in BMNH 1930.7.1.238). Both posterior fangs are missing, and the tips of the anterior fangs are broken. As in BMNH 1930.7.1.238, the tips of the maxillae are edentulous and the teeth are blunt.

The left dentary of BMNH 1930.7.1.238 has the following tooth formula: 4(5-6)-7 = 13. The right dentary of this specimen appears pathological; it has seven anterior teeth followed by a large interspace (no sockets) and one additional tooth. Dentary formulae for the holotype (BMNH 1946.1.12.28) are 4(5-6)-8 = 14 (right) and 4(5-7)-8 = 15 (left). No dentary diastema is present in either specimen. The tips of the dentaries are edentulous, just as in the maxillae, but that characteristic is scarcely visible in lateral view (Fig. 12) because of the mesial curvature of the anterior tip of the bone.

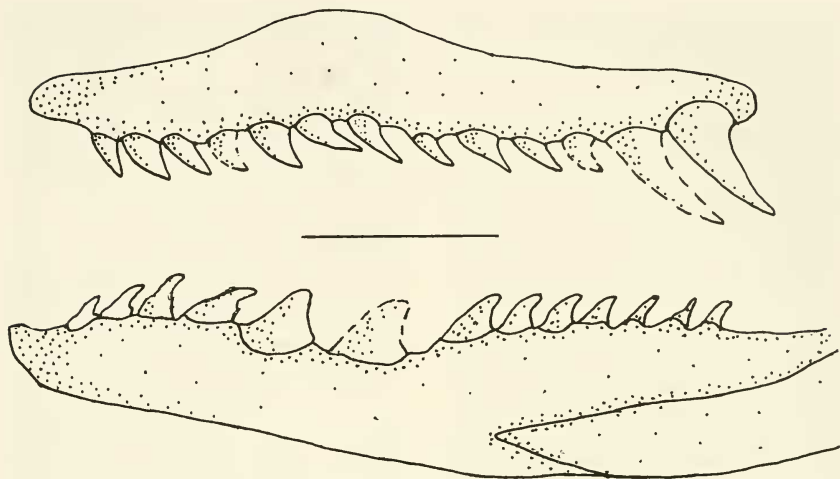


Figure 12. Right maxilla (reversed) and left dentary of *Heteroliodon occipitalis* (BMNH 1930.1.238). Teeth drawn with dotted lines are missing. Note the unusual edentulous anterior portion of the maxilla. Scale bar = 1 mm.

The maxillary teeth in *Heteroliodon* except for the fangs and the dentary teeth except for the median enlarged pair are hinged and have a mobility comparable to species of *Pseudoxyrhopus*.⁹ As in *Pseudoxyrhopus*, the anterior teeth in each bone appear more distinctly hinged than the posterior teeth. Individual teeth in *Heteroliodon* are short, blunt, distally slightly expanded in a transverse plane, and anteroposteriorly compressed at the tips. The tooth bases are enlarged, a morphology similar to that of some species of *Liophidium* (see photographs in Savitzky, 1981). There is also a suggestion of a bony pedicel to which the teeth attach, another

feature also observed in other hinged-tooth snakes (Savitzky, 1981).

The edentulous tips to the maxillae and dentaries in *Heteroliodon* are unusual and of unknown significance. The maxillae abut posterolateral extensions of the premaxillary bone and are bound to them by strong fibrous tissue; this tissue may play a role in strengthening the snout during burrowing, which is indicated by the few natural observations for this species (Raxworthy and Nussbaum, 1994) and by the similarities to other burrowing snakes in the overall form of the snout and head (see Cadle and Greene, 1993, table 25.1). I am unaware of other snakes in which the anterior end of the maxilla is edentulous except some species in the African genus *Prosymna* (Broadley, 1980: 486). Perhaps only coincidentally, this observation is nevertheless intriguing because *Prosymna* is a specialized predator of reptile eggs (Broadley, 1979, 1980) and one other species of the *Pseudoxyrhopus* group at least occasionally eats reptile eggs. Unfortunately

⁹ The posterior enlarged dentary tooth on the left side of the holotype is loose and might be interpreted as hinged. However, I suspect this loose tooth reflects a stage in normal tooth shedding because the corresponding teeth in BMNH 1930.7.1.238 are firmly ankylosed. The interpretation of the other maxillary and dentary teeth as hinged is based on the fact that all teeth are kinetic, rather than the usual snake condition in which alternate teeth are mobile, reflecting the normal replacement cycle.

ly, no dietary data are available for *Heteroliodon* and whether this unusual character is correlated with such a diet is unknown.

In summary, the dentition of *Heteroliodon* is unusual in the following characters: (1) edentulous tips to the maxilla and the dentary, (2) gap of variable width separating the fangs from anterior maxillary teeth, (3) enlarged median series of dentary teeth, (4) teeth hinged except for the enlarged maxillary and dentary teeth, and (5) unusual overall tooth form.

Hemipenis

The right inverted hemipenis of BMNH 1930.7.1.238 was studied in situ through a previous midventral incision in the tail and a medioventral incision in the ventral lobe of the right hemipenis. The hemipenis extends to the level of the suture between subcaudal scales 7 and 8 (7.5 mm total length) and divides at the level of the suture between subcaudals 4 and 5 (4 mm from the base). Thus, it is approximately 45% bilobed. The sulcus spermaticus divides at the level of the suture between subcaudals 3 and 4 (3 mm from the base) and apparently passes to the tip of the lobes in the dorsolateral wall of the organ (centrolineal in orientation). The base of the organ below the sulcus division has a sparse covering of small spinules or spinulate papillae. At the point of sulcus division on the asulcate side are approximately two rows of relatively large straight spines. Distal from this point the spines first abruptly and then more gradually decrease in size toward the tips of the lobes. The tips of the sulcus spermaticus end in a relatively large nude area on the tips of the lobes. Aside from the nude tips and the apparently nude crotch of the organ, the lobes are entirely spinose (no calyces). No other conspicuous features, such as pockets or nude areas, are present.

The hemipenis of *Heteroliodon* resembles that of *Pseudoxyrhopus oblectator*, including the following characters: (1) relatively enlarged spines at the point of divi-

sion of the sulcus spermaticus, decreasing distally from that point, (2) basal region sparsely covered with minute spines, (3) crotch of organ nude, and (4) nude tips to the lobes. The nude apical areas appear relatively larger in *Heteroliodon* than in *P. oblectator*, but it is difficult to quantitatively compare inverted and everted organs.

REVISED DIAGNOSES AND COMMENTARY

Raxworthy and Nussbaum (1994: 3, 25, 30) briefly diagnosed *Pseudoxyrhopus*, *Heteroliodon*, and *Pararhadinaea* (including *Exallodontophis albignaci* within *Pararhadinaea*) using, in part, characters of the dentition and relative eye size. However, the reinterpretation of dentitional characters and taxonomic revisions reported herein require modification of these diagnoses insofar as tooth characters are concerned. In addition, I believe relative eye size is only a proxy for overall body size and cannot be used as a diagnostic generic character.

Raxworthy and Nussbaum's (1994) diagnosis of *Heteroliodon occipitalis* included having anterior and posterior dentary teeth of equal sizes, maxillary fangs only "slightly enlarged," and a "large" eye (0.35 versus <0.3 times head depth). All of these character states were considered different from those in *Pseudoxyrhopus*. Scoring of the relative size of the fangs in *Heteroliodon* was based on a damaged specimen. The fangs of *Heteroliodon* are more than twice the size of the other maxillary teeth (Fig. 12) and are proportionally as large as those of *Pseudoxyrhopus*. Similarly, Raxworthy and Nussbaum stated that in *Pararhadinaea* the anterior and posterior dentary teeth were equal in size and erroneously attributed some other dentitional characters to *Pararhadinaea* that are characteristic only of *Exallodontophis albignaci*. In *Pararhadinaea melanogaster* the posterior dentary teeth are much larger than the anterior ones, whereas in *Exallodontophis albignaci*, upon which Raxworthy and Nussbaum based

their diagnosis of *Pararhadinaea*, the anterior and posterior dentary teeth are more nearly the same size.

Moreover, the relative sizes of the anterior and posterior dentary teeth and relative eye size differ among species of *Pseudoxyrhopus* in a manner that diminishes their utility in distinguishing the genera. In effect, both are apparently related to body size, and the smaller species of *Pseudoxyrhopus* are more nearly like *Heteroliodon* and *Pararhadinaea* in both characters. For example, in *Pseudoxyrhopus oblectator* the anterior and posterior dentary teeth (i.e., those anterior and posterior to the median enlarged series) are about the same size. In *P. ambreensis*, *P. imerinae*, *P. kely*, *P. quinquelineatus*, and *P. sokosoko* the anterior teeth are equal to or only slightly larger than the posterior teeth. The size distinction between the anterior and posterior dentary teeth is most obvious in the large species of *Pseudoxyrhopus*, *P. microps* and *P. tritaeniatus*, in which the anterior teeth are very elongate (Fig. 6). The general pattern in the dentary teeth, as noted by Boulenger (1890), is an increase in tooth size to the median enlarged series and then an abrupt decrease. However, the size increase in the anterior series may be abrupt, as in *P. tritaeniatus* (Fig. 6), or more gradual, as in *P. imerinae*, *P. oblectator*, and *P. quinquelineatus*. In *P. quinquelineatus* the anterior and posterior dentary teeth are approximately the same size. In any case, because of size variation within the anterior and posterior series, a qualitative distinction in size between the series is imprecise.

The few data on relative eye diameter (RED; eye diameter divided by head depth) preclude adequate statistical evaluation, but several observations suggest that RED is also size related. My reevaluation of RED in these snakes was prompted by comparison of the adult (RED = 0.3) and juvenile (RED = 0.34) specimens of *Pseudoxyrhopus oblectator*. The juvenile value is indistinguishable from that of *Heteroliodon* (0.35) when

measurement error is considered. Other data indicating that RED is related to size include (all data from Raxworthy and Nussbaum [1994] except *Pseudoxyrhopus oblectator* and juvenile *P. tritaeniatus*) (1) the species of *Pseudoxyrhopus* with the largest RED (*P. kely*, *P. sokosoko*, *P. oblectator*; RED = 0.27–0.34) are among the smaller species; (2) *Heteroliodon* and *Pararhadinaea* have larger REDs (0.29–0.35) but are as small or smaller than the smallest species of *Pseudoxyrhopus* (*Exallodontophis albignaci*, with RED = 0.15–0.2, is an exception to the pattern); (3) juveniles of at least two species of *Pseudoxyrhopus*, *P. oblectator* (MCZ 181287) and *P. tritaeniatus* (AMNH 60712), have larger REDs (0.34 and 0.42, respectively) than adults (0.30 and 0.26, respectively); and (4) although *Exallodontophis albignaci* clearly has a smaller RED than the other genera, RED within this species also shows an inverse relationship with body size (SVLs of 240 mm, 253 mm, and 370 mm with corresponding REDs of 0.20, 0.19, and 0.15). Thus, *Pararhadinaea*, *Heteroliodon*, and the small species of *Pseudoxyrhopus* have eye sizes that might be considered typical for their body sizes, and relative eye size is therefore only an approximate proxy for body size.

Taking these observations into consideration, the tooth characters used to diagnose *Pseudoxyrhopus*, *Heteroliodon*, and *Pararhadinaea* can be restated. After removal of "*Pararhadinaea*" *albignaci* to *Exallodontophis*, *Pararhadinaea* can be characterized much as done originally by Boettger (1898):

—Maxillary teeth approximately 14–16, equally spaced (no diastema), gradually increasing in size anterior to posterior, with the last two teeth somewhat enlarged, compressed, and ungrooved. Dentary teeth 12–14 with approximately the last half of the series larger and more robust than the anterior teeth; posterior dentary teeth widely spaced. Overall tooth form unusual: tips blunt and compressed. Teeth hinged.

The most distinctive feature of the dentition of *Heteroliodon* and the most diffi-

cult to explicitly describe is the overall tooth form. Otherwise, its dentition can be briefly characterized:

—Maxillary teeth 10–11+2. Anterior maxillary teeth subequal followed by two greatly enlarged, ungrooved fangs; fangs preceded or not by a gap less than one tooth in width. Anterior tip of maxilla edentulous. Dentary teeth 13–15: two or three median dentary teeth enlarged. Overall tooth form highly unusual: tips blunt, compressed anteroposteriorly, and distally flared in a transverse plane. Teeth hinged.

Pseudoxyrhopus is the most difficult to characterize because of interspecific variation in tooth form and dentitional morphology. The teeth vary from long and slender in the large species such as *P. tritaeniatus* (Fig. 6) to rather shorter and less pointed as in *P. quinquelineatus* and *P. oblectator*. Nevertheless, the following characterization applies to the dentition of all species of *Pseudoxyrhopus*:

—Maxillary teeth 12–17+2. Anterior maxillary teeth subequal or slightly larger anteriorly; short diastema present or not, followed by two greatly enlarged, ungrooved fangs. Dentary teeth 15–20, with a median series of two or three enlarged teeth usually followed by a short diastema. Teeth hinged except in adults of some species, including at least *Pseudoxyrhopus tritaeniatus*.

**A NEW HYPOTHESIS FOR THE
RELATIONSHIPS OF
PSEUDOXYRHOPUS,
EXALLODONTOPHIS, HETEROLIODON,
AND PARARHADINAEA: LIOPHIDIUM AS
A MEMBER OF THE
PSEUDOXYRHOPUS GROUP**

Previous Hypotheses and Characters

Raxworthy and Nussbaum (1994: 34, table 7) tabulated characters shared by *Pseudoxyrhopus*, *Heteroliodon*, and *Pararhadinaea* (although their tabulations for *Pararhadinaea* were based primarily on *Exallodontophis albignaci*). Only one of their characters linking these genera, the series of enlarged median dentary teeth, is unquestionably derived. However, Raxworthy and Nussbaum possibly erred in scoring this as a character of *Pararhadinaea* be-

cause, as clarified above, the state of this character in the type species is ambiguous (Fig. 7), thus making enlarged median dentary teeth a character unambiguously shared only by *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* (some other Malagasy genera, e.g., *Dromicodryas*, *Ithycyphus*, and *Langaha* have enlarged anterior dentary teeth). The other shared characters noted by Raxworthy and Nussbaum (1994, table 7) are highly variable among colubrids (e.g., ungrooved, enlarged maxillary fangs) or variable within *Pseudoxyrhopus* and/or *Heteroliodon*, as shown herein (e.g., maxillary diastema). This study adds two other unquestionably derived characters shared by all four genera: hinged teeth and a modified pattern of tooth replacement. Both are also characteristic of *Liophidium*. A dentary diastema is shared by *Exallodontophis* and *Pseudoxyrhopus*.

Thus, the case that all four genera, *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea*, form a clade relative to other snakes is not compelling based on present evidence because the only previously identified synapomorphy (enlarged median dentary teeth) unambiguously applies only to the first three genera, and two other apomorphies (hinged teeth and modified tooth replacement) apply to these four genera and to *Liophidium*. A consideration of other characters of these snakes reinforces the ambiguous relationship of *Pararhadinaea* to the other genera. I first reconsider Raxworthy and Nussbaum's (1994) claim of a "significant" morphological gap between these and other Malagasy colubrid genera because it bears on the interpretation of the relationships of the group.

Raxworthy and Nussbaum (1994: 34) speculated that the sister group of *Pseudoxyrhopus*–*Heteroliodon*–*Pararhadinaea* would be a non-Malagasy colubrid because of perceived "significant morphological and behavioral differences of [these genera] compared to the other Malagasy genera." These perceived differences were

dentition (ungrooved maxillary teeth), body form (low relative head to neck width, "rounded head profile"), and general habits (nocturnal, terrestrial). However, these features often differ considerably among closely related snakes and even substantially within a genus in some cases. Numerous examples exist, but cases illustrating considerable divergence in some or all of these sorts of features include *Epicrates* (Kluge, 1989), *Xenodontini* (Myers, 1986), *Sibon* and *Dipsas* (Peters, 1960; Kofron, 1980), and *Rhadinaea-Coniophanes-Pliocercus* (Myers, 1974). Even within *Pseudoxyrhopus* the differences in head shape between *P. inermis* and *P. quinquelineatus* and the other species is substantial. It is premature to exclude other Malagasy genera as potential sister taxa of *Pseudoxyrhopus*-*Heteroliodon*-*Pararhadinaea* on the basis of these superficial characteristics. In any case it is unclear in what context these characters differ "significantly" from other Malagasy colubrids because all are observed elsewhere in those snakes.

Hinged Teeth and Tooth Replacement Pattern as Evidence for a Clade of Malagasy Snakes

The discovery of hinged teeth and a modified pattern of tooth replacement in *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* and some ontogenetic stages of all examined species of *Pseudoxyrhopus* makes comparison with *Liophidium* inevitable because these derived characters are observed in many, if not most, species of *Liophidium* (Savitzky, 1981; personal observations). The occurrence of hinged teeth in these genera might be viewed as independent adaptations to a diet of hard-bodied lizard prey. Alternatively, the common possession of clearly derived features such as these could indicate a close relationship of the genera (or parts thereof). These two interpretations are not mutually exclusive. For example, the presence of an enlarged median series of dentary teeth is a possible adaptation associated with feed-

ing mode but also may be a synapomorphy indicating close relationship of *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon*. Because hinged teeth and modified tooth replacement are patently derived characters shared by a small group of Malagasy colubrids, I accept at face value that these characters originated once in the Malagasy snake fauna and thus are strong evidence that *Liophidium*, *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* comprise a monophyletic clade, which I refer to as the *Pseudoxyrhopus* group.

If we accept the hinged teeth and modified tooth replacement as evidence that *Liophidium* is closely related to the other genera, how should we view the "significant morphological and behavioral differences" between *Liophidium* and the other genera perceived by Raxworthy and Nussbaum (1994)? Although the difference in habitus between the large species of *Pseudoxyrhopus* (*P. tritaeniatus*, *P. microps*, *P. ankafinaensis*; all >850 mm SVL) and species of *Liophidium* is impressive, it is perhaps no more so than that between the large and small species of *Pseudoxyrhopus* (six species have maximal SVLs of <400 mm and two others are ≤510 mm; data from Raxworthy and Nussbaum, 1994). The two largest species of *Liophidium*, *L. therezieni* and *L. vaillanti*, attain SVLs of at least 600 mm and 532 mm, respectively. The largest specimens of five other species of *Liophidium* were 187–454 mm SVL (unpublished observations). Moreover, *Heteroliodon occipitalis* and *Pararhadinaea melanogaster* are among the smallest Malagasy colubrids, and *P. melanogaster* is superficially similar to some species of *Liophidium*.

Similarly, my perception is that the small species of *Pseudoxyrhopus* (e.g., *P. ambreensis*, *P. sokosoko*, and *P. kely*; maximum SVLs of 180–333 mm) are not so different from some species of *Liophidium* in head shape, body proportions, and general habitus, as a superficial comparison readily shows (Figs. 13–15). Several species of *Lio-*

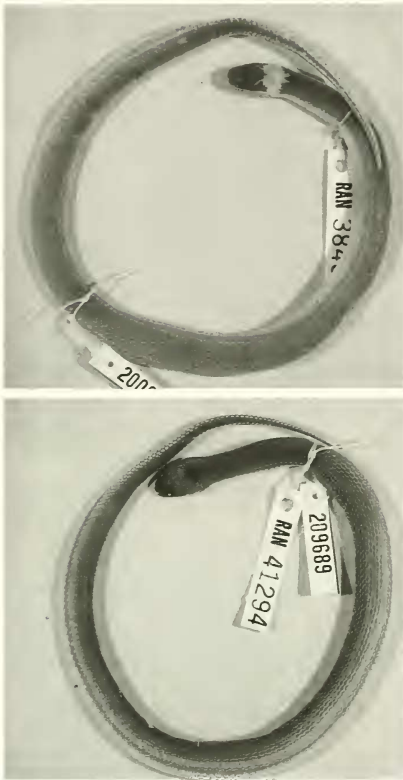


Figure 13. Two small species of *Pseudoxyrhopus*. Both approximately $\times 0.95$. Top: *P. ambrensis* (UMMZ 200062, total length = 344 mm). Bottom: *P. sokosoko* (UMMZ 209689, total length = 323 mm). *Pseudoxyrhopus sokosoko* is one of the species of *Pseudoxyrhopus* lacking a pale nape collar. Both approximately $\times 0.95$.

phidium attain body sizes as large or larger than those of some species of *Pseudoxyrhopus* (e.g., *L. vaillanti*, *L. torquatum*, *L. therezieni*, and *L. rhodogaster* all attain SVLs of >420 mm). Species of *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* have short tails (11–22% of total length), whereas in *Liophidium* relative tail lengths are much more variable (12–27% of total length; personal observa-

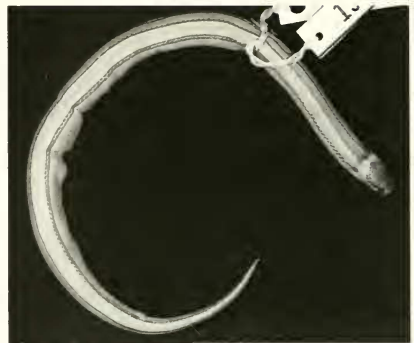


Figure 14. *Pseudoxyrhopus kely* (UMMZ 192022; juvenile male paratype; total length = 184 mm.). This is the smallest species of *Pseudoxyrhopus* (the holotype and only other known specimen is an adult male 217 mm in total length). Approximately $\times 1.2$.

tions). As in species of *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea*, the head in *Liophidium* is only slightly distinct from the neck, pupils are round, and the species are terrestrial to cryptozoic (several species of *Pseudoxyrhopus* may be burrowers; Raxworthy and Nussbaum, 1994: 33). The point of these comparisons is not to suggest that these similarities provide evidence of relationship but only that a perception of “significant morphological differences” among these snakes based on superficial characteristics is not especially clear.

Of course, activity patterns do differ among the genera. All species of *Pseudoxyrhopus*, *Heteroliodon*, and *Exallodontophis* are probably nocturnal, whereas *Pararhadinaea melanogaster* (probably) and species of *Liophidium* are diurnal (personal observations for *Liophidium*; see also footnote 7 and discussion of character 11 for *Pararhadinaea*). This behavioral character was thought by Raxworthy and Nussbaum (1994) to further distance these genera from other Malagasy colubrids.¹⁰ However, divergence in activi-

¹⁰ Raxworthy and Nussbaum (1994) stated that *Par-*

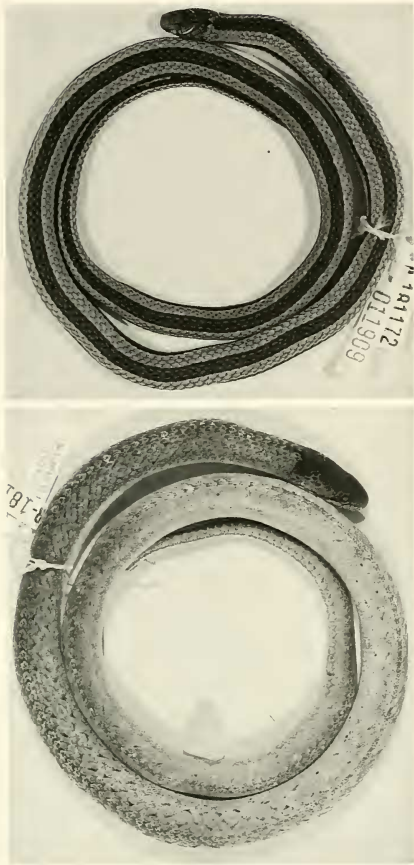


Figure 15. Adults of two of the larger species of *Liophidium*. Top: *Liophidium rhodogaster* (MCZ 181172, total length = 533 mm). Bottom: *Liophidium torquatum* (MCZ 181305, total length = 654 mm).

ity pattern is known to occur among closely related snakes (even varying geographi-

arhadinaea was nocturnal. However, as with their statements concerning dentition for this genus, this behavioral statement is based on observations for *Exallodontophis albignaci*. *Pararhadinaea melanogaster* is probably diurnal, as indicated by a single observation (see discussion of character 11).

cally or seasonally within some species; see Cadle and Greene, 1993). One could even speculate that the divergence in activity pattern between *Liophidium* and the other genera might have been promoted by their presumed strong overlap in dietary resources (see Schoener, 1989, for discussion of divergence in activity pattern as a response to dietary overlap). This divergence would be predicated only on their shared food resource and not on any special evolutionary relationship between the snakes.

In Madagascar, terrestrial to cryptozoic snakes such as *Pseudoxyrhopus* would encounter few other nocturnal snake competitors. Aside from the nocturnal members of the *Pseudoxyrhopus* group and *Madagascarophis* (medium-size to large terrestrial snakes, usually one species per locality), Madagascar's snake fauna is essentially devoid of terrestrial nocturnal snakes (in contrast to arboreal nocturnal snakes of the genera *Geodipsas*, *Lycodryas*, and *Stenophis*). Nevertheless, it does seem implausible that skinks or gerrhosaurids are such limiting resources as to have effected competition (and therefore temporal divergence in activity) between *Liophidium* and nocturnal species of the *Pseudoxyrhopus* group; these lizards are abundant in areas where the snakes occur. Regardless of the factors responsible for differences in the diel cycles of *Liophidium* and the other genera, this difference alone is insufficient grounds for considering the snakes distantly related.

In conclusion, I see no special morphological disparity between *Pseudoxyrhopus*, *Heteroliodon*, *Exallodontophis*, and *Pararhadinaea* and other Malagasy colubrids. I suggest that the hinged teeth and modified tooth replacement provide evidence of a relationship of these snakes with *Liophidium*. Thus, *Liophidium* itself is part of a larger radiation of snakes in Madagascar that manifests a variety of dentional specializations associated in snakes with feeding on hard-bodied lizard prey: hinged teeth (all genera), enlarged median dentary teeth (*Pseudoxyrhopus*, *Exallodonto-*

phis, *Heteroliodon*), diastema in the dentary tooth row (*Pseudoxyrhopus*, *Exallodontophis*), enlarged median maxillary teeth and broad diastema (*Exallodontophis*), and peculiar tooth form (*Heteroliodon*, *Pararhadinaea*, *Liophidium*). The available dietary data, although lacking for most species, are consistent with a shared behavioral repertoire correlated with the morphological characteristics. However, although all of these snakes share the basic dental modification of hinged teeth, the other characters are distributed mosaically among the genera. Thus, if these snakes are a clade exclusive of other Malagasy snakes, the evolution of novel dental and jaw characteristics among them has been quite remarkable.

Comparisons of Other Character Systems in *Liophidium* and the Other Genera

Do other characters offer support for inclusion of *Liophidium* in the *Pseudoxyrhopus* group? Aside from the synapomorphies provided by the dentition, too little is known of other potentially informative character systems to meaningfully compare them. Although hemipenial variation among species of *Pseudoxyrhopus* appears to be minimal, hemipenial variation among species of *Liophidium* is much greater, and some species of *Liophidium* have unusual features such as asymmetry of the hemipenial lobes or basal pockets and lobes (Domergue, 1983; Cadle, 1996a: 392; see also Ziegler et al., 1996).¹¹ Nev-

ertheless, hemipenes of *Liophidium*, *Heteroliodon*, and *Pseudoxyrhopus* are similar in being deeply bilobed and entirely spinose, with a centrolineal sulcus spermaticus extending to the tips of the lobes. Domergue's (1983, fig. 5A) illustration of the hemipenis of *L. therezieni* is very similar to that of *P. oblectator* (Fig. 5), and he mentioned (Domergue, 1983: 1117) nude tips to the lobes of the hemipenis of *L. vaillanti* (which I confirmed on MCZ 22203) that seem similar to those I observed in *P. oblectator* and *Heteroliodon occipitalis*. *Liophidium rhodogaster* also has relatively large nude areas on the tips of the lobes, but these are lacking in *L. torquatum* (personal observations), although *L. torquatum* does have a very tiny patch devoid of spines at the tip of each lobe. Otherwise, the morphology of these hemipenes is very generalized and lacking in clear apomorphies based on present knowledge. The superficial similarity between them may be nothing more than that. Hemipenes of a wide array of African and Malagasy colubrids could be characterized as "bilobed, spinose, and with a centrolineal sulcus spermaticus," but substantive comparisons are presently precluded because detailed descriptions of most taxa are lacking. Unfortunately, hemipenes of *Exallodontophis* and *Pararhadinaea* are unknown apart from Domergue's (1984) uninformative comment that the hemipenis of *Exallodontophis albignaci* was spinose. Nonetheless, the presence of

¹¹Ziegler et al. (1996) described the hemipenis of *Liophidium torquatum*, but two of its most unusual characteristics were not mentioned. First, *L. torquatum* (MCZ 181305) has a very deep, elongate nude pocket adjacent to the undivided basal portion of the sulcus spermaticus; it extends from the base of the organ to a level just short of the division of the sulcus spermaticus. The pocket is surrounded by a thickened, somewhat raised border, which is produced into a low lobe on the absulate edge. Second, the large spines at the base of the hemipenial lobes on the sulcate side of the organ are surmounted on a pair of large globose tuberosities that are clearly set apart from and project above the surrounding tissue of the lobes and base of the hemipenis. Such tuber-

osities are unknown in other Malagasy snakes. Neither of these features of the hemipenes of *L. torquatum* have been described in other species of *Liophidium* (Domergue, 1983; Ziegler et al., 1996), and they do not occur in *L. rhodogaster* (personal observations of MCZ 181170), whose hemipenis has yet to be described. An unusual characteristic of the hemipenes of several species of *Liophidium* is asymmetry in the length of the lobes. Ziegler et al. (1996) reported slight asymmetry in *L. torquatum*, which I confirmed in MCZ 181305, but the lobes in *L. rhodogaster* (MCZ 181170) are symmetrical. Both *L. torquatum* and *L. rhodogaster* have centrolineal sulci spermatici, which seems to be the case for the species figured by Domergue (1983).

TABLE 4. MAXILLARY DENTITION IN *LIOPHIDIUM*. BILATERAL COUNTS ARE GIVEN WHEN AVAILABLE.

Species/specimens	Tooth count ¹
<i>L. aperti</i> ,	
MNHN 1982.442 (type)	24+3
<i>L. chaubadi</i>	
MNHN 1978.2789 (type)	25+2
MNHN 1978.2788	25+3 ²
<i>L. rhodogaster</i>	
MCZ 180381	31+2
MCZ 180382	32+2
MCZ 181169	31+2
MCZ 181170	34+2
MCZ 181171 (Fig. 16)	32+2, 31+2
MCZ 181172	30+2
<i>L. therezieni</i>	
MNHN 1982.444 (type)	27+3
MNHN 1978.1425	30+3
<i>L. torquatum</i>	
BMNH 1946.1.1.38 (type)	29+2
MCZ 180303	28+2
MCZ 181305	25+2
<i>L. trilineatum</i> ,	
BMNH 1946.1.15.66 (type)	24+2
<i>L. vaillanti</i>	
MNHN 1901.186 (syntype)	24+3
MNHN 1901.187 (syntype)	23+4
MCZ 22203 (Fig. 16)	21+4, 21+4

¹No. regular teeth + no. enlarged posterior teeth (which are only slightly enlarged compared with the immediately anterior maxillary teeth) (see Fig. 16).

²This count is much greater than the count given by Domergue (1984), who reported 19 total teeth.

the unusual nude apical morphology of the hemipenes of some members of the *Pseudopyrhopus* group may provide another synapomorphy for this hypothesized clade or parts thereof.

Savitzky (1981) noted that the posterior-most maxillary teeth of *Liophidium rhodogaster* were larger and less effectively hinged than the other teeth. In fact, slight enlargement of posterior maxillary teeth seems to be the rule in *Liophidium*, and two to four posterior teeth may be enlarged (Table 4; Fig. 16).¹² In *Liophidium*

these enlarged teeth are only slightly larger than the immediately anterior teeth. They do not approach the size or abrupt enlargement of the rear fangs of *Pseudopyrhopus*, *Exallodontophis*, or *Heteroliodon*, which are always much larger than any other maxillary teeth (Figs. 6, 10, 12).

The degree of enlargement of the posterior maxillary teeth varies among species of *Liophidium*. For example, the posterior teeth of *L. vaillanti* are relatively more enlarged than those of *L. aperti*, *L. chaubadi*, or *L. rhodogaster* (Fig. 16). Although *Liophidium* lacks a maxillary diastema, the holotypes of *L. torquatum* and *L. trilineatum* each have a small gap separating the enlarged teeth from more anterior ones (this character seems to be variable at least in *L. torquatum*; two other specimens lacked such a gap). As noted by Savitzky (1981), the enlarged posterior teeth in *Liophidium* are akinetic or have reduced kinesis as compared with more anterior teeth.

Liophidium and *Pararhadinaea melanogaster* are very similar in the morphology of individual teeth (rather blunt, distally compressed and flared transversely) and in the general morphology of the maxilla and its dentition (teeth gradually increasing in size, with two or more somewhat enlarged posterior teeth, no diastema) (cf. Figs. 7, 16). In contrast, the posterior maxillary teeth in *Exallodontophis*, *Heteroliodon*,

three "feebly enlarged" teeth in the type of *L. trilineatum*, whereas I recorded two, Mocquard (1902) reported that the last "6 or 7" teeth in the syntypes of *L. vaillanti* were "a little longer and more robust" than the others (I recorded three and four enlarged teeth in the two specimens). These discrepancies probably reflect the mainly gradual anterior to posterior enlargement of maxillary teeth in *Liophidium*. The point upon which all authors seem to agree is that some of the posterior teeth in *Liophidium* are enlarged to a variable extent in the different species. This seems to be a somewhat uncommon morphology in colubrids, but it is observed in geographically and taxonomically diverse genera, e.g., the *godmani* group of *Rhadinaea* (Myers, 1974: 28-29) and some species of *Leptophis* (Oliver, 1948: 175-176).

¹² In *Liophidium* the relative enlargement of the posterior maxillary teeth is subtle and sometimes subjective. For example, Boulenger (1896: 598) recorded

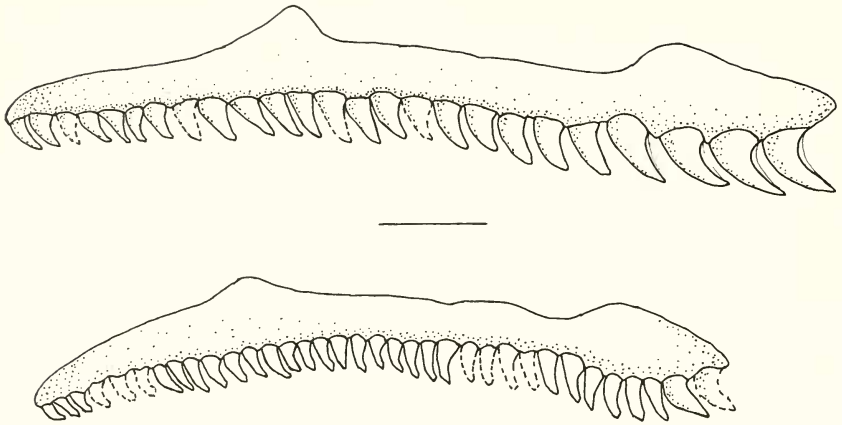


Figure 16. Maxillary dentition of two species of *Liophidium*. Teeth drawn with dotted lines are missing. Scale bar = 1 mm. Top: *Liophidium vaillanti* (MCZ 22203), left maxilla. Bottom: *Liophidium rhodogaster* (MCZ 181171), left maxilla.

and *Pseudoxyrhopus* are greatly enlarged and often separated by a diastema from the anterior teeth, which usually are subequal or even slightly decrease slightly in size anterior to posterior. The similarities in dentition between *Pararhadinaea* and *Liophidium* account for resolution of these genera as a clade in one of the most parsimonious trees discussed in the next section.

Although I explicitly hypothesize a close relationship of *Liophidium* with *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* on the basis of the shared derived characters of hinged teeth and modified tooth replacement, I am not the first to link *Liophidium* with some of these other genera. Mocquard (1909), without stating reasons, postulated that *Pararhadinaea* was "very close" to [*Liophidium*] *vaillanti* (then in the monotypic genus *Idiophis*), noting only that in the former the maxillary teeth increase in size from front to back, whereas in the latter they were subequal (this is more or less true if one ignores the enlarged posterior fangs in *L. vaillanti*; cf. Figs. 7, 16). Mocquard was perhaps impressed with the

similarity in maxillary dentition. The dentition of *Liophidium* and *Pararhadinaea* seems to be an uncommon (if not unique) arrangement among Malagasy colubrids. At about the same time Werner (1909) suggested, again for obscure reasons, that his new genus *Rhabdotophis* (= *Pararhadinaea*) was "perhaps closely related to *Pseudoxyrhopus*." Werner's reasoning is especially obscure because none of the species of *Pseudoxyrhopus* known at the time resemble *Pararhadinaea*, although *Pseudoxyrhopus kely*, discovered much later (Raxworthy and Nussbaum, 1994), is superficially similar in size and color pattern to *Pararhadinaea* (see Figs. 8, 9, 14).

CHARACTER DISTRIBUTIONS IN THE PSEUDOXYRHOPUS GROUP

Recognition of *Liophidium* as part of the *Pseudoxyrhopus* group and consideration of the new and corrected morphological data reported herein permits a more detailed analysis of relationships among these snakes than has been attempted before. To estimate the phylogeny of the *Pseudoxyrhopus* group I coded

TABLE 5. DISTRIBUTION OF SELECTED CHARACTERS AMONG *PSEUDOXYPHOPUS*, *EXALLODONTOPHIS*, *HETERO-LIODON*, *PARARHADINAEA*, AND *LIOPHIDIUM*. HYPOTHETICAL ANCESTRAL STATES WERE INFERRED AS DISCUSSED IN THE TEXT FOR EACH CHARACTER. CHARACTER POLARITIES FOR THE INGROUP ARE NOT IMPLIED EXCEPT FOR CHARACTERS IN WHICH THE ANCESTOR WAS CODED AS 0 OR 1. ALTERNATIVE SCORINGS OF SOME CHARACTERS ARE GIVEN IN BRACKETS; UNBRACKETED CODINGS ARE REFERRED TO AS "STANDARD." 01 = POLYMORPHISM, ? = UNCERTAIN.

Character	<i>Pseudoxyrhopus</i>	<i>Exalloodontophis</i>	<i>Heteroliodon</i>	<i>Pararhadinaea</i>	<i>Liophidium</i>	Ancestor
1. Hinged teeth	1 [01]	1	1	1	1	0
2. Tooth replacement	1	1	1	1	1	0
3. Median dentary teeth	1	1	1	0 [1]	0	0
4. Dentary diastema	1 [01]	1	0	0	0	0
5. Maxillary teeth	1	1	1	1	0	?
6. Maxillary fangs	1	1	1	0	0	? [1]
7. Maxillary diastema	01	1	0	0	0	?
8. Head pattern	1	1	1	0	0	0
9. Dorsal scales	1	0	0	0	0 [01]	?
10. Posterior reduction	0	1	1	1	01	?
11. Diel behavior	1	1	1	0 [?]	0	?
12. Body size	01	0	0	0	0	?
13. Tooth form	0	0	1	1	1	0
14. Anterior dentary teeth	0	0	0	1	0	0
15. Number of posterior dentary teeth	01	0	0	0	1	?
16. Number of ventral scales	01	0	0	0	01	?

many of the morphological characters discussed above.

Table 5 shows the distribution of characters used for phylogenetic analysis among the Malagasy snakes with hinged teeth. A few autapomorphic characters are included (e.g., character 14) because they have figured prominently in the previous discussions of dentition herein or because my interpretations differ from those given by Raxworthy and Nussbaum (1994). However, other known autapomorphies are not included because they do not contribute to resolution of a phylogeny, although they do aid in diagnosing terminal taxa (e.g., the edentulous anterior extension of the maxilla in *Heteroliodon*). Also, I have ignored characters that do not vary within the ingroup (e.g., absence of grooving on the fangs) even though other character states occur in other Malagasy colubrids.

For some characters more than one scoring was possible depending on how the character was interpreted for particular taxa. These alternatives are indicated in brackets in Table 5. Alternative scorings

were included in separate phylogenetic analyses. Three of five alternative scorings (characters 1, 4, 9) were from a single state to polymorphism within a terminal taxon and did not affect the resulting most parsimonious tree topologies but did affect tree lengths and measures of consistency. The other alternative scorings (characters 3, 6, 11) were for alternative states in *Pararhadinaea* and the ancestor.

Characters 1 and 2 provide evidence for the monophyly of the *Pseudoxyrhopus* group (five genera listed in Table 5), defined as the ingroup for the phylogenetic analyses. Because explicit outgroups for this putative clade are as yet unknown, I reconstructed a hypothetical ancestor for purposes of tree rooting. Ancestral states were hypothesized for some characters on the basis of known variation among Malagasy colubrids or colubrids generally. For other characters, ancestral states were not readily apparent and these were coded as unknown (?) in the phylogenetic analyses. The specific rationale for each character is given below. A more detailed discussion of dentition characters (characters 1–7, 13–

15) was given in preceding sections. Character states for *Liophidium* are based in part on unpublished data (see also Domergue, 1983). In the following discussion the state designations 0 and 1 are conveniences with no implication as to which is ancestral or derived, although 0 was assigned to the ancestral state when that could be reasonably inferred.

1. *Teeth are firmly ankylosed (0) or hinged (1)*. All ingroup taxa have hinged teeth. Although adults of *Pseudoxyrhopus tritaeniatus* have firmly ankylosed teeth, juveniles have hinged teeth, as do all other specimens of *Pseudoxyrhopus* examined. Thus, I coded *Pseudoxyrhopus* as state 1, under which the adult condition of *P. tritaeniatus* is interpreted as a reversal, but I also used an alternative coding of polymorphism (01). The ancestor is assumed to have state 0.

2. *Tooth replacement is alternate (0) or modified (1)*. Alternate tooth replacement is the usual condition in colubrids. Tooth replacement in all ingroup taxa is modified. The ancestral condition is assumed to be 0.

3. *Dentary teeth are subequal (0) or a median series may be enlarged (1)*. The condition of *Pararhadinaea* is somewhat ambiguous, and I scored it as 0 and alternatively as 1 for purposes of analysis. In any case, the morphology of the dentary teeth of *Pararhadinaea* is not similar to that of *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* (state 1). Alternatively, *Pararhadinaea* could be scored with an autapomorphy for this character, which would not affect tree topologies. The ancestral condition is assumed to be 0.

4. *A diastema in the dentary tooth row may be absent (0) or present (1)*. *Heteroliodon*, *Pararhadinaea*, and *Liophidium* lack a dentary diastema (0), whereas in *Exallodontophis* a diastema is present (1). Virtually all *Pseudoxyrhopus* examined have a diastema (1) (Table 2); because one specimen lacks a diastema I also used the alternative coding of polymorphic (01). The ancestral condition is assumed to be

0 because dentary diastemata are unknown in other Malagasy colubrids and are otherwise extremely rare in colubrids.

5. *Maxillary teeth more than 25 (0) or less than 20 (1)*. As with any continuously varying quantitative character, discretely coded states are somewhat arbitrary (see Gift and Stevens, 1997, for discussion and references). All species of *Liophidium* have more than 25 teeth (Table 4), whereas no species of the other genera have more than 19 (data presented here and unpublished observations for *Pseudoxyrhopus*). Thus, I arbitrarily coded two states (>25 or <20). Actual ranges are *Pseudoxyrhopus* (14–19),¹³ *Exallodontophis* (8–10), *Heteroliodon* (12 or 13), *Pararhadinaea* (13 or 14), *Liophidium* (26–33). The ancestor is coded as unknown (?) because Malagasy colubrids show a broad range of maxillary tooth numbers, which is approximately encompassed by the numbers in the *Pseudoxyrhopus* group (*Exallodontophis* and species of *Liophidium* representing the lower and higher extremes, respectively).

6. *Posterior maxillary fangs may be slightly enlarged as compared with the other maxillary teeth (0) or greatly enlarged (1)*. In *Pararhadinaea* and *Liophidium* the fangs are only slightly enlarged as compared with the immediately preceding teeth (0) (Figs. 7, 16). In *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* the fangs are greatly enlarged as compared with the immediately preceding maxillary teeth (1) (Figs. 6, 10, 12) (the greatly enlarged median maxillary teeth of *Exallodontophis* are ignored in scoring this char-

¹³ Raxworthy and Nussbaum (1994: 3) reported a range of 9–18 maxillary teeth in *Pseudoxyrhopus*. The lower value was apparently based on the holotype of *P. kely*, which I did not examine (the total count is at least 10 because they missed one of the posterior fangs in this species). However, my tooth counts are almost invariably greater than those given by Raxworthy and Nussbaum, and my tooth count for the paratype of *P. kely* and one specimen of *P. sokosoko* were 12+2, which are the lowest values I obtained (Table 2).

acter). State 0 is rare among Malagasy colubrids. Apart from *Pararhadinaea* and *Liophidium*, only *Dromicodryas* and *Micropisthodon* have this state, whereas all other genera have state 1. The state in the hypothetical ancestor is unknown (?). However, Savitzky (1981) postulated a derivation of *Liophidium* from snakes with greatly enlarged posterior fangs based on the feebly enlarged posterior teeth in *Liophidium*; this state was used as an alternative coding for the ancestor in the phylogenetic analyses.

7. A maxillary diastema may be absent (0) or present (1). *Pseudoxyrhopus* is scored as polymorphic (01) because of intraspecific variation. *Liophidium* and *Pararhadinaea* lack a maxillary diastema (state 0), whereas *Exallodontophis* has a diastema (state 1). In *Heteroliodon* a small gap was present in one specimen (no gap in another specimen), but I scored it as 0 because the gap is less than the width of a tooth. The ancestral condition is unknown (?), although a diastema is more commonly present in Malagasy colubrids.

8. A pale labial stripe continuous from the rostral scale to the nape collar is absent (0) or present (1). *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* are coded 1, whereas *Pararhadinaea* and *Liophidium* are coded 0. A labial stripe complete from the rostral scale to the nape collar is an unusual pattern, and the ancestor is scored 0.

In *Heteroliodon*, *Exallodontophis*, and all species of *Pseudoxyrhopus* a white stripe begins on the rostral scale, traverses the upper labials, and is continuous with a light nape collar except in those species of *Pseudoxyrhopus* lacking a collar (Fig. 17; see also Figs. 1, 2, 11, 14; and figures and descriptions by Raxworthy and Nussbaum, 1994; Nussbaum et al., 1998). In virtually all individuals (*Heteroliodon* and some individual *Pseudoxyrhopus* are exceptions) a peculiar short spur extends dorsally across the lateral edges of each internasal scale from the rostral portion of the stripe (Figs. 2, 17). The stripe is sometimes interrupted

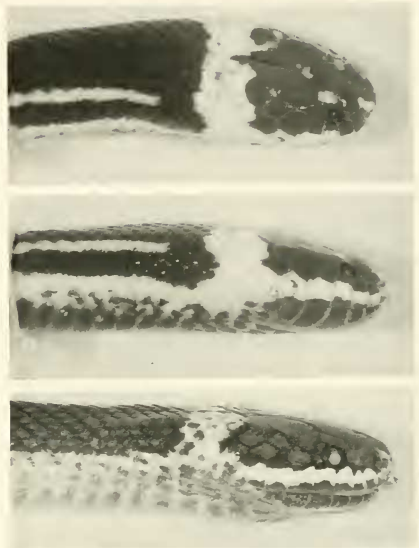


Figure 17. Labial and head patterns in the *Pseudoxyrhopus* group (see character 8). Approximately $\times 2.27$. Top to bottom: Dorsal view of the head of *Exallodontophis albignaci* (UMMZ 203642), lateral view of the head of *E. albignaci* (UMMZ 203642), and lateral view of the head of *Pseudoxyrhopus oblectator* (MCZ 182292; holotype). The unusual pale spurs across the lateral edges of the internasals are visible in both specimens (less distinct in the *P. oblectator* due to camera angle).

below the eye and, rarely, by a dark spot on the rostral scale. The stripe is vivid (not obscured by a wash of dark pigment, as occurs commonly in colubrids) and usually is bordered above and below by black pigment (in *Heteroliodon* the labial border is white and thus the ventral border of the labial stripe is not defined).

Some variation is found within *Pseudoxyrhopus*. The internasal spurs are lacking in the only known specimen of *P. ankafinaensis* and occasional specimens of *P. tritaeniatus*, whereas in some specimens of *P. microps* and *P. tritaeniatus* the spurs broaden and completely surround the nostrils. In juveniles of *Pseudoxyrhopus microps* and in an adult with a very indistinct collar (CM 119068) the labial stripe and

collar are continuous (Raxworthy and Nussbaum, 1994, fig. 14). *Pseudoxyrhopus heterurus*, *P. ineriniae*, *P. quinquelincatus*, and *P. sokosoko* lack collars in known specimens, but the labial stripe otherwise has the same disposition as in the collared species (juveniles of *P. heterurus* are unknown, but juveniles of the other three lack distinct collars; Fig. 13). In *P. quinquelincatus* the entire anterior portion of the snout is involved in the extensions of the labial stripe, and this may be true in *P. ineriniae* (the only specimen examined was very faded).

In *Pararhadinaea* an irregular light labial stripe may be present or the supralabials may be irregularly spotted. However, when a stripe is present it is less discrete than in the other three genera and is obscured by a dense suffusion of dark pigment; it is separated from a nape collar by a broad dark postocular stripe that is continuous with dorsolateral stripes on the body (Fig. 18). Species of *Liophidium* often have light labial stripes, but these generally do not continue across the rostral scale and often end well short of it. Nape collars are present only in some species of *Liophidium* (e.g., in *L. therezieni* and some individuals of *L. rhodogaster*); when present they are usually at least partially separated from the labial stripe by a narrow dark band or row of spots.

9. *Midbody scale rows are 17 (0) or 19 or more (1)*. *Pararhadinaea*, *Heteroliodon*, and *Exallodontophis* have 17 scale rows (0), whereas *Pseudoxyrhopus* has 19–25 (1). All Malagasy species of *Liophidium* have 17 midbody scale rows, although *L. mayottensis* from the Comoro Islands has 19; separate analyses were conducted coding *Liophidium* as 0 or as polymorphic (01). The ancestral condition is uncertain (?).

10. *The number of dorsal scale rows may be the same posteriorly as at midbody (0) or dorsal scales may undergo posterior reduction (1)*. Dorsal scales are not reduced in *Exallodontophis*, *Heteroliodon*, or *Pararhadinaea* (0), whereas they under-

go posterior reduction involving scale rows 4 and/or 5 in all species of *Pseudoxyrhopus* (1). Some species of *Liophidium* undergo posterior reduction involving rows 4 or 5, whereas other species are unreduced; thus, *Liophidium* is scored as polymorphic (01). The ancestral condition is unknown (?).

11. *Activity patterns are either diurnal (0) or nocturnal (1)*. All observations indicate that species of *Liophidium* are diurnal (0), whereas *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* are nocturnal (1). A single observation for *Pararhadinaea melanogaster* suggests that it may be diurnal (0), although in separate analyses it was also scored as uncertain (?). Because the ancestral condition is unknown, the ancestor was also scored as uncertain (?).

Raxworthy and Nussbaum (1994) stated that *Pararhadinaea melanogaster* was probably nocturnal, but definitive observations are available only for MNHN 1982-1220; these data indicate that *P. melanogaster* is probably diurnal. Charles P. Blanc (in litt., 11 February 1999), who collected MNHN 1982-1220, provided the following observations paraphrased from his field notes:

—The snake was collected on the coast 19 December 1972, in native forest on the ground. . . . I found this snake in the morning. As far as I can remember it was in the middle of the morning and the snake was active, perhaps disturbed by myself or by the trees [being cleared]. The snake was collected among logs and wood cut material in a splendid lowland evergreen rainforest just being cut down, near the front of clearing on a sandy beach intended to become an industrial coconut plantation.

Thus, although these data do not rule out the possibility of the snake being disturbed from seclusion, taken at face value they indicate diurnality for *Pararhadinaea melanogaster*.

The three observations for *Heteroliodon* include being caught in a pitfall trap (time of day not reported), within a granite crevice, and within a rotten log, all during the day (Raxworthy and Nussbaum, 1994: 27–

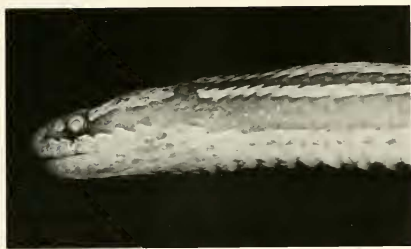


Figure 18. Lateral view of the head and anterior body of *Pararhadinaea melanogaster* (MNHN 1982-1220, holotype of *P. m. marojejensis*). Note the lack of a discrete light labial stripe and the dark bar separating the light colors of the upper labials and nape. Compare with Figure 17. Approximately $\times 4.8$.

28). I interpret these to indicate nocturnality for this species, as did Raxworthy and Nussbaum (1994: 33). *Exallodontophis albignaci* was collected dead on a road in the morning, probably killed the previous night (Domergue, 1984); it was also caught in pitfall traps (time of day not reported) and within the soil under a large log during the day (Raxworthy and Nussbaum, 1994). As with *Heteroliodon*, I interpret these observations to indicate nocturnality.

12. Adult SVL is less than 650 mm (0) or greater than 800 mm (1). All species of *Liophidium*, *Pararhadinaea*, *Heteroliodon*, and *Exallodontophis* have state 0 (greatest SVLs 600 mm, 202 mm, 268 mm, 370 mm, respectively). Most species of *Pseudoxyrhopus* are <650 mm adult SVL (state 0), whereas *P. microps*, *P. tritaeniatus*, and *P. ankafinaensis* attain sizes >800 mm adult SVL (state 1). *Pseudoxyrhopus* is thus scored as polymorphic (01). The ancestral state is uncertain (?).

13. The morphology of individual teeth is unmodified (0) or modified (1). The teeth of *Pseudoxyrhopus* are curved, sharply pointed, and continuously tapering toward the tips (Fig. 6), which is the usual condition in colubrids and other caenophidians (state 0). These characters vary slightly among the species of *Pseudoxyrhopus*. For example, the teeth in *P. quinquelineatus* and *P. imerinae* are straighter,

more robust, and less sharply pointed than those in the other species. The dentary teeth in *Pseudoxyrhopus* are usually straighter than the maxillary teeth (Fig. 6). However, the teeth of *Heteroliodon*, *Pararhadinaea*, and *Liophidium* are short, relatively straight, and have blunt tips that are slightly compressed anteroposteriorly. The distal portion of each tooth is slightly flared compared with the middle; thus, the teeth do not taper continuously toward the tips. This is considered a modified condition (state 1). Savitzky (1981, fig. 1i) illustrated the morphology for *Liophidium*, which is basically similar to that of *Heteroliodon* and *Pararhadinaea*.¹⁴ However, the teeth of *Exallodontophis* are in some respects intermediate between the extremes represented by *Liophidium* and *Pseudoxyrhopus*. The anterior maxillary teeth of *Exallodontophis* are short, relatively straight, and rather blunt, but their tips are not expanded or compressed to the degree in *Liophidium*. In contrast, the anterior dentary teeth of *Exallodontophis* are straight, stout, rather bluntly pointed, and slightly compressed. The condition in *Exallodontophis* is thus somewhat ambiguous but is more similar to the condition in *Pseudoxyrhopus* and is scored 0. The ancestral condition is assumed to be 0 because the modified tooth morphology is unknown in other Malagasy snakes and is rare in colubrids generally.

14. The anterior dentary teeth are subequal to or larger than the posterior dentary teeth (0), or the posterior dentary teeth are larger and more robust than the anterior teeth (1). *Pseudoxyrhopus*, *Exallodontophis*, and *Heteroliodon* have state 0 (Figs. 6, 10, 12). *Pararhadinaea melanogaster* has state 1 (Fig. 7). *Liophidium* is

¹⁴ Tooth form varies somewhat among species of *Liophidium*, and the morphology in *L. rhodogaster* illustrated by Savitzky (1981) is the extreme. In other species the teeth are blunt and compressed at the tips, but the degree of distal expansion varies. For example, in both *L. torquatum* and *L. vaillantii* the anterior maxillary teeth are more expanded distally than the posterior teeth (personal observations).

scored as 0 for this character even though no distinction is made between anterior and posterior dentary teeth; all dentary teeth are subequal. The ancestral condition is assumed to be 0. Raxworthy and Nussbaum (1994, table 7) stated that the anterior dentary teeth were larger than the posterior ones in *Pseudoxyrhopus* but not in *Heteroliodon* or *Pararhadinaea*. Their scoring for *Pararhadinaea* was based on *Exallodontophis albignaci*, and my observations for both *Heteroliodon* (Fig. 12) and *Exallodontophis* are that the anterior and posterior dentary teeth are approximately the same size (state 0).

15. *The number of posterior dentary teeth is less than 10 (0) or more than 12 (1).* *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* have state 0, whereas *Pseudoxyrhopus* is polymorphic (01) (see footnote 3, Table 2). I coded *Liophidium* as state 1 because of the large number of dentary teeth in general, even though there is no distinction between the anterior and posterior dentary teeth. The ancestral state is uncertain (?).

16. *The number of ventral scales is less than 200 (0) or more than 200 (1).* *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* have state 0, whereas both *Pseudoxyrhopus* and *Liophidium* are interspecifically variable and are coded as polymorphic (01). The ancestral state is uncertain (?).

PHYLOGENY OF THE PSEUDOXYRHOPUS GROUP

Parsimony analysis of the data matrix (Table 5) using the standard character codings resulted in three equally most parsimonious trees (MPTs) of 21 steps (Fig. 19). Trees 1 and 2 (Fig. 19) are fully resolved, whereas tree 3 has an unresolved basal polytomy. The three trees differ in the placement of *Pararhadinaea*, and the strict consensus of all three MPTs is identical to tree 3. The MPTs had a CI (excluding uninformative characters) of 0.68 and an RI of 0.89. Phylogenetic trees using the alternative polymorphism codings for

characters 1, 4, and 9 (Table 5) yielded four MPTs of 24 steps (CI excluding uninformative characters = 0.67; RI = 0.87). Three of these trees had topologies identical to the MPTs using the standard codings; the fourth was identical to tree 2 (Fig. 19) except that it contained a polytomy for *Pseudoxyrhopus*–*Exallodontophis*–*Heteroliodon*.

Either of two alternative character codings force resolution of the MPT for the data as either tree 1 or tree 2 (Fig. 19). These alternatives are, respectively, for character 3 (*Pararhadinaea* = state 1) and character 6 (ancestor = state 1), resulting in single MPTs of 21 steps in each case when no alternative polymorphic character codings are used. In the first case, the alternative coding results in another synapomorphy shared by *Pararhadinaea* and *Pseudoxyrhopus*–*Exallodontophis*–*Heteroliodon* (*P-E-H*) (tree 1). In the second case, coding the ancestral condition of the maxillary fangs the same state as that shared by *P-E-H* results in recognition of the state 0 shared by *Pararhadinaea* and *Liophidium* as a synapomorphy (tree 2). Thus, the phylogenetic position of *Pararhadinaea* is ambiguous, and it seems preferable to consider the strict consensus topology (Fig. 19, tree 3) as the best current estimate of phylogeny for the *Pseudoxyrhopus* group.

In any case, the hypothesis of monophyly for *Pseudoxyrhopus*–*Heteroliodon*–*Pararhadinaea* to the exclusion of other Malagasy colubrids (Raxworthy and Nussbaum, 1994), including *Liophidium*, is not strongly supported when characters shared with *Liophidium* are considered. If *Liophidium* is excluded from the analysis, a single MPT is obtained. It has 17 steps and a topology identical to the trees in Figure 19 with *Liophidium* pruned from them.

The ambiguous relationship of *Pararhadinaea* to the other genera under consideration emphasizes how few characters support a clade containing *Pseudoxyrhopus*, *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea* to the exclusion of *Liophi-*

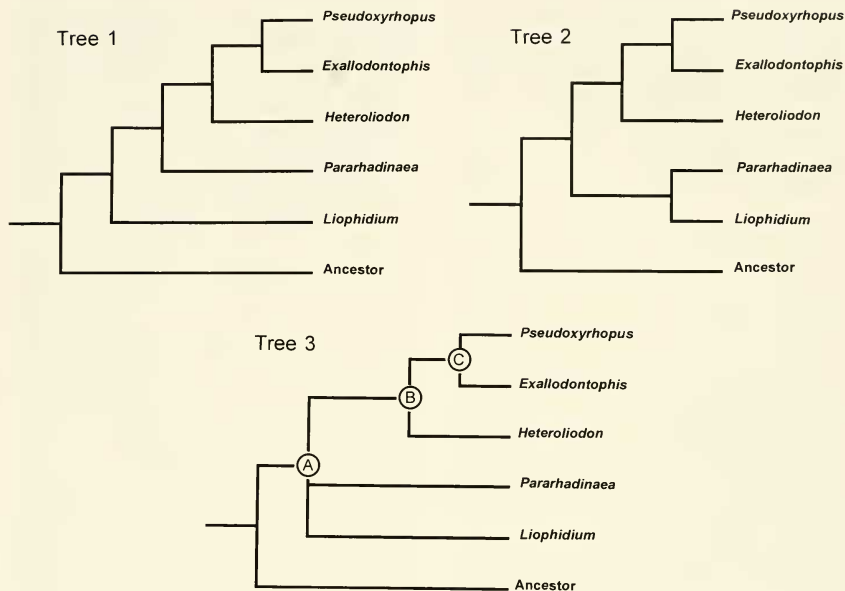


Figure 19. Three equally parsimonious trees reconstructed from the standard codings of character data in Table 5. Tree length = 21 steps, CI (excluding uninformative characters) = 0.68, RI = 0.89. The strict consensus of all three trees is identical to tree 3. Nodes A–C in tree 3 are referred to in the text and in Table 6.

dium. Although only characters 1 and 2 (Table 5) unambiguously support the inclusion of *Liophidium* in the *Pseudoxyrhopus* group, support for inclusion of *Pararhadinaea* in the group is equally weak. Only character 5 is an apomorphy supporting the relationship of *Pararhadinaea* to *P-E-H* in tree 1 (Fig. 19) under either ACCTRAN or DELTRAN character optimization. However, for tree 2 (Fig. 19) only character 13 under DELTRAN optimization supports the clade *Pararhadinaea*–*Liophidium*. Further resolution of the relationships of *Pararhadinaea* will not be possible without the addition of other characters or elimination of uncertain (?) codings for ancestral character states (accomplished objectively by more definitive resolution of outgroups). Eliminating the uncertain codings for some characters in

Table 5 would make either of the fully resolved topologies (Fig. 19, trees 1 and 2) more favorable under parsimony (e.g., characters 5, 6, 7, 11).

None of the MPTs (Fig. 19) places *Exallodontophis albignaci* and *Pararhadinaea melanogaster* as sister taxa, as would be implied by the union of both species in *Pararhadinaea* according to the previous taxonomy. In fact, the shortest trees constraining monophyly of these two taxa are 6 steps longer than the MPTs using the standard character scorings (five trees of 27 steps; CI excluding uninformative characters = 0.54; RI = 0.22). This analysis provides strong support for removal of *albignaci* from *Pararhadinaea*.

Table 6 shows apomorphies under ACCTRAN optimization for clades in the strict consensus phylogeny (Fig. 19, tree 3,

TABLE 6. APOMORPHIES FOR THE STRICT CONSENSUS OF RELATIONSHIPS AMONG GENERA OF THE *PSEUDOXYRHOPUS* GROUP (SEE FIG. 19, TREE 3, FOR LABELED NODES). STANDARD CHARACTER CODINGS (TABLE 5) WERE OPTIMIZED USING ACCTRAN UNDER MAXIMUM PARSIMONY.

Branch	Character no. ¹	Change
Ancestor \leftrightarrow node A ²	1	0 \leftrightarrow 1
	2	0 \leftrightarrow 1
	13	0 \leftrightarrow 1
Node A \rightarrow node B	3	0 \Rightarrow 1
	6	0 \Rightarrow 1
	8	0 \Rightarrow 1
	11	0 \Rightarrow 1
Node B \rightarrow node C	4	0 \Rightarrow 1
	7	0 \rightarrow 1 ³
	13	1 \Rightarrow 0
Node C \rightarrow <i>Pseudoxyrhopus</i>	9	0 \Rightarrow 1
	10	1 \Rightarrow 0
Node A \rightarrow <i>Pararhadinaea</i>	14	0 \Rightarrow 1
Node A \rightarrow <i>Liophilidium</i>	5	1 \Rightarrow 0
	15	0 \Rightarrow 1

¹Characters 12 and 16 change within terminal taxa (*Pseudoxyrhopus* and/or *Liophilidium*) and thus do not appear in the table.

²Direction of change between ancestor and node A is not determinable.

³This change is not the only most parsimonious reconstruction possible, but all others are unambiguous changes.

standard character codings). The clade *P-E-H* is the most strongly supported, with four unambiguous character transformations supporting it. Each of these transformations is unique and unreversed using the present character codings, but resolution of the uncertain (?) codings for the ancestor could change that assessment. Unambiguous synapomorphies of the clade *P-E-H* are enlarged median dentary teeth, greatly enlarged maxillary fangs, and the distinctive head pattern. *Pseudoxyrhopus* and *Exallodontophis* are united by one unique and unreversed synapomorphy (the presence of a diastema in the dentary tooth row, character 4) and a reversal (tooth form, character 13). Change in character 7 (maxillary diastema) along the branch between nodes C and D (Table 6) occurs only because ACCTRAN was used and *Pseudoxyrhopus* is polymorphic for this character. Character 13 is the only

character for which a disparity between the minimum possible changes (1) and the estimated tree changes (2) exists.

Another character potentially corroborating the clade *Pseudoxyrhopus-Exallodontophis* relative to *Heterohiodon* is the presence of pale spurs across the lateral portions of the internasals from the rostral scale (see discussion of character 8). I did not code this unusual feature separately, considering it part of the labial stripe complex. However, despite some variation within *Pseudoxyrhopus*, this character would map to the branch between nodes B and C (Fig. 19, tree 3) and offers additional support for the sister relationship of *Pseudoxyrhopus* and *Exallodontophis*.

CHARACTER EVOLUTION AND RELATIONSHIPS WITHIN THE *PSEUDOXYRHOPUS* GROUP

The phylogenetic hypotheses in Figure 19 bear on previous discussions of character evolution and relationships within *Pseudoxyrhopus*. Regardless of the coding of the hypothetical ancestor, reconstructed plesiomorphic conditions for the *Pseudoxyrhopus* group (basal ingroup node in Fig. 19) and for *Pseudoxyrhopus* itself include small body size (character 12), fewer than 11 posterior dentary teeth (character 15), and fewer than 200 ventral scales (character 16). The contrasting derived conditions of the *Pseudoxyrhopus microps* group (including *P. microps*, *P. tritaeniatius*, and *P. ankafinaensis*) confirm the hypothesis that the *P. microps* group is monophyletic within *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994); these species are also unique among *Pseudoxyrhopus* species in having 25 midbody dorsal scale rows, which is probably a derived character because of its rarity among Malagasy colubrids. (Alternative interpretations of other character variation within *Pseudoxyrhopus* result in some other hypotheses of relationships than those given by Raxworthy and Nussbaum, 1994.)

More interesting from the standpoint of natural history are implications of the phy-

logenetic hypotheses in Figure 19 for the evolution of dentitional characters. Setting aside the hinged teeth and modified tooth replacement characteristic of all these snakes, only species of *Pseudoxyrhopus* lack unusual characteristics of dental configuration or of the morphology of individual teeth; their dental characters do not immediately suggest features not observed elsewhere among many colubrids (Fig. 6). This is not the case for the other genera. *Exallodontophis* is characterized by the highly unusual form of the maxilla, an exceptionally broad maxillary diastema, and unusually large median maxillary teeth (Fig. 10). *Pseudoxyrhopus*, the sister group of *Exallodontophis*, and *Heteroliodon*, the immediate outgroup of *Pseudoxyrhopus*–*Exallodontophis*, share a similar configuration of the maxillary dentition (Figs. 6, 12). Thus, the unusual dentitional characteristics of *Exallodontophis* probably evolved from a condition in which the number of maxillary teeth was already somewhat reduced (character 5), but the other unusual characters evolved within the *Exallodontophis* lineage.

The peculiar form of the teeth in *Heteroliodon*, *Pararhadinaea*, and *Liophidium* (character 13) has a more complex evolutionary history under any of the hypotheses in Figure 19. Tree 1 requires that the derived tooth morphology either evolved twice (once in *Heteroliodon* and once in *Pararhadinaea*–*Liophidium*) or was a plesiomorphic state for the *Pseudoxyrhopus* group that was subsequently lost in the lineage leading to *Pseudoxyrhopus* and *Exallodontophis*. Either of the hypotheses illustrated in trees 2 and 3 (Fig. 19) requires a basal origin and subsequent reversal of the unusual tooth morphology shared by these genera. However, a less parsimonious hypothesis is that the unusual tooth morphology is nonhomologous in these genera, i.e., it has evolved multiple times within this group. Thus, not only does this small group of Malagasy colubrids show exceptional diversity in tooth characters and the overall configuration of the den-

tion, but the phylogenetic hypotheses suggest a complex evolutionary history (multiple origins or reversals) for some individual characters (tooth form, maxillary diastema) but not others (enlarged dentary teeth and maxillary fangs). Precisely how the evolution of these characters is correlated with prey acquisition behaviors remains to be determined.

MONOPHYLY OF TERMINAL TAXA

One implicit assumption in this (and indeed all) phylogenetic analyses is the monophyly of the terminal taxa. This assumption is not problematic for *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea*; the derived dentitional morphologies for these monotypic genera have already been documented. The assumption is more problematic for *Pseudoxyrhopus* and *Liophidium*. The combination of characters given for the diagnosis of *Pseudoxyrhopus* (Raxworthy and Nussbaum, 1994) includes mostly rather common colubrid characters (enlarged, ungrooved rear fangs), although the presence of 19 or more midbody scale rows and posterior scale reduction (introduced herein) distinguish it from *Exallodontophis*, *Heteroliodon*, and *Pararhadinaea*. However, *Pseudoxyrhopus* is characterized mainly by lacking the autapomorphies of the other genera. Other character systems need to be investigated to properly diagnose *Pseudoxyrhopus*.

Two of the most widely cited characters diagnosing *Liophidium* (seven described and several undescribed species) are hinged teeth and modified tooth replacement. These characters are now seen as synapomorphies for a larger clade of Malagasy snakes (Table 6). There seems to be much variation in size, body proportions (e.g., relative tail lengths), scale characters, tooth morphology (Savitzky, 1981), and hemipenial morphology (Cadle, 1996a: 382) within *Liophidium*. Earlier in this century (e.g., Mocquard, 1909), the species of *Liophidium* were partitioned among *Liophidium*, *Polyodontophis*, and *Idiophis*, distinguished primarily on the

basis of characters of the maxillary and dentary dentition. Guibé (1958) placed the Malagasy species of all these genera in *Liophidium* and stated that the rationale was to be given in a separate publication to be coauthored with A. R. Hoge. That report was never published, but early diagnoses for these genera (e.g., Boulenger, 1893, 1896; Mocquard, 1901) show little distinction. For example, the only character that differs in Boulenger's diagnoses of *Liophidium* and *Polyodontophis* is whether the posterior teeth are "feebly enlarged" or not, which is rather variable and subjective.

Other characters sometimes cited as synapomorphies for *Liophidium* (anterior displacement of the dentary-compound bone articulation in the lower jaw, free posterior dentigerous process on the dentary, highly developed intramandibular kinesis, long lateral process of premaxillae overlapping anterior ends of maxillae) have been verified in few species because of their rarity in collections. Virtually all comparative studies have been based on the species *L. rhodogaster*, *L. torquatum*, and *L. vaillanti* and often only one or two of these (Morgan, 1973; Savitzky, 1981, 1983; Domergue, 1983; Cadle, 1996a: 381–382). Until these putative synapomorphies and other characters are surveyed for a broader array of species the monophyly of *Liophidium* will remain poorly corroborated. For example, it is quite possible that some of the "diagnostic" characters of *Liophidium* actually document the monophyly of a smaller set of species, just as the hinged teeth and tooth replacement pattern corroborate the monophyly of a larger set. Thus, the character interpretations presented here should be considered provisional, and additional comparative study of species of *Liophidium* should be undertaken. One character of potential significance in diagnosing *Liophidium* is the asymmetry of the hemipenial lobes, which has been noted in several species (e.g., Domergue, 1983; Ziegler et al., 1996; see also footnote 11). This un-

usual character may prove diagnostic for *Liophidium*, but given that hemipenes of *Pararhadinaea* and *Exallodontophis* are as yet undescribed, asymmetry of lobes may also be more widespread within the *Pseudoxyrhopus* group.

ARE THE MALAGASY AND AFRICAN HINGED-TOOTH SNAKES CLOSELY RELATED?

The phylogeny and hypothesized character evolution in Figure 19 are based on few, albeit highly unusual, characters shared by *Liophidium* and *Pseudoxyrhopus*–*Exallodontophis*–*Heteroliodon*–*Pararhadinaea* (*P-E-H-P*). Nonetheless, I question the significance of morphological and behavioral differences between *P-E-H-P* and other Malagasy colubrids, specifically *Liophidium*, as emphasized by Raxworthy and Nussbaum (1994). Thus, I am dubious that the closest relatives of *P-E-H-P* or the *Pseudoxyrhopus* group should be sought outside Madagascar. Despite these reservations, additional comparisons between the *Pseudoxyrhopus* group and the African genera said to be related to *Lycophidion* and *Mehelya* are probably warranted because many of their dentitional characters are similar, although in various combinations in the different genera (personal observations; see also Parker, 1933). These African genera, Group II of Bogert (1940), are *Hormonotus*, *Gonionotophis*, *Mehelya*, *Lycophidion*, and *Chamaelycus*.

Both the maxillary and dentary dentitions of Bogert's (1940) Group II genera are similar in many unusual characters to those of some members of the *Pseudoxyrhopus* group. Like the *Pseudoxyrhopus* group, hinged teeth are found in *Lycophidion*, *Mehelya*, and *Chamaelycus*. At least some species of *Lycophidion*, *Mehelya*, *Chamaelycus*, and *Hormonotus* have a broad diastema in the middle of the maxilla, which is preceded by relatively enlarged robust teeth (Parker, 1933). However, neither the diastema nor the teeth preceding it are developed to the same degree as in *Exallodontophis*. *Lycophidion*,

Mehelya, *Chamaelycus*, and *Hormonotus* also have an anterior series of dentary teeth that increase in size to about the fifth or sixth tooth, followed by a series of smaller teeth (Bogert, 1940; Parker, 1933; personal observations). In *Chamaelycus*, *Hormonotus*, and some species of *Lycophidion* a median pair of dentary teeth is exceptionally enlarged and is followed by a diastema, as in *Pseudoxyrhopus* and *Exallodontophis*. Despite these shared unusual characters, none of which appear in precisely the same combinations as in the *Pseudoxyrhopus* group, the morphology of the dentition and dentigerous bones in Bogert's Group II genera is otherwise dissimilar to that in any Malagasy colubrids. For example, the African genera lack enlarged posterior fangs. Some similar dental characters (median maxillary diastema and enlarged anterior dentary teeth) are also found in other African snakes, such as some members of Bogert's (1940) Group I (e.g., *Lamprophis olivaceus*; Boulenger, 1893, fig. 22). These characters led Boulenger (1890) to hypothesize that *Pseudoxyrhopus* was related to these "lycodonts," a large, nebulous assemblage, but he was not more specific.

An additional complication in evaluating possible relationships between the *Pseudoxyrhopus* group and Bogert's (1940) Group II is that the monophyly of Group II has not been extensively documented. Bogert explicitly deemphasized hemipenial characters in his classification except the divided or undivided nature of the sulcus spermaticus. His groups represented a subjective impression of genera "believed to represent the most closely allied forms" (Bogert, 1940: 10). McDowell (1987), without extensive commentary, implicitly set apart *Mehelya* and *Gonionotophis* from a cluster of genera including *Lycophidion*, *Chamaelycus*, *Hormonotus*, and *Bothrolycus*, the last of which Bogert (1940) had included in his Group I. In the only biochemical study of this group, Cadle (1994) found no support for a strong association of either *Lycophidion* or *Gonionotophis*

specifically with *Mehelya*, the only member of Group II represented by a reference antiserum, when their albumins were compared by microcomplement fixation (no samples of the other Group II genera were available). Too much should not be made of these unidirectional immunological comparisons, although reciprocity and rate-tested data were considered reliable in that study. Also, in Cadle's (1994) study, Bogert's Groups I and II formed a well supported clade. Thus, although Cadle (1994) found no support for a phyletic association between *Lycophidion* or *Gonionotophis* and *Mehelya*, all of these genera were part of a larger well-supported clade. This result suggests that relationships among these genera might be more complex than suggested by Bogert's groupings. In particular, the morphology of the hemipenis and dentition of *Gonionotophis* is unlike that of the other genera of Group II, but we currently lack a comprehensive understanding of the phylogenetic significance of these characters in African colubrids.

Bogert (1940) had examined hemipenes of all Group II genera except *Gonionotophis*, whose hemipenis seems not to have been described in detail. Hemipenes of all Group II genera except *Gonionotophis* are deeply divided (bilobed) and entirely spinose and have centrifugal sulci spermatici. However, the hemipenis of *Gonionotophis granti* is nonbilobed or very shallowly bilobed and has an unusual nude apical structure with a shallow delimiting groove on the asulcate side and a divided sulcus spermaticus with centrifugal branches (personal observations based on the fully everted organs of MVZ 176439). McDowell (1987: 37) independently noted the "hardly bilobate" structure of the hemipenis in *G. granti*. Except for the centrifugal branches of the sulcus spermaticus, these features are unlike those of any other members of Group II. Furthermore, at least two species of *Mehelya*, *M. crossi* and *M. guirali*, have a large basal nude pocket, which has not been reported in other gen-

era of Group II (personal observations on the inverted organs of MVZ 75748 and MVZ 81462, respectively). The nonbilobed organ and unusual apical structure of *Gonionotophis* are probably derived features (see Myers, 1973; Cadle, 1996b). Thus, the closest relatives of *Gonionotophis* might be sought among other African colubrids with nonbilobed hemipenes rather than among Group II genera, although one cannot exclude the possibility that these characters are simply autapomorphies of *Gonionotophis* within Group II. Nonetheless, *Gonionotophis* differs in other significant ways from the Group II genera.

Notably, all genera of Group II except *Gonionotophis* have a diastema in the middle of the maxillary tooth row and have enlarged median dentary teeth and a dentary diastema. Loveridge (1939) seems to have been the first to specifically suggest a relationship between *Gonionotophis* and *Mehelya*, but his inference was based solely on the confused synonymy of species in the two genera in the 19th century literature: "From this [i.e., the confused species and generic synonymies] it will be concluded that the relationship between the two genera . . . is of the closest nature" (Loveridge, 1939: 131). Loveridge presented no morphological data to bolster this conclusion. *Gonionotophis* and *Mehelya* do share unusual lateral expansions on the vertebrae, although these are not as extensively developed in *G. granti* as in *M. capensis* and *M. crossi* (personal observations); *Gonionotophis* also lacks the prezygopophysal expansions observed in *Mehelya* (personal observations; see Bogert, 1964). However, none of these unusual vertebral characters are known in the other Group II genera. The immunological data and the differences in dentition and hemipenial morphology between *Gonionotophis* and *Mehelya* suggest that a relationship between these two genera may be more remote than current wisdom suggests. The only dietary records for *Gonionotophis* are two frogs (Shine et al.,

1996). This record contrasts with the primarily reptilian (especially lizard) diets characteristic of the other Group II genera (Parker, 1933; Branch, 1976; Savitzky, 1981; Broadley, 1983; Shine et al., 1996), although *Mehelya* is known to occasionally consume frogs, especially bufonids (Shine et al., 1996).

Hemipenial morphology of *Lycophidion*, *Mehelya*, and other Group II genera except *Gonionotophis* are similar to those of *Pseudoxyrhopus* and *Liophidium* only in superficial ways that do not suggest special relationship. The known hemipenes of *Lycophidion* and *Mehelya* are deeply bilobed and entirely spinose (for descriptions and illustrations, see Bogert, 1940; Doucet, 1963; Branch, 1976; personal observations). Hemipenes of *Lycophidion* and *Mehelya* differ from those of any known Malagasy colubrids in having centrifugal sulci spermatici, which divide more basally in most species of *Lycophidion* and *Mehelya* than in *Pseudoxyrhopus* and *Heteroliodon* (Doucet, 1963; Broadley, 1983; personal observations of *M. crossi* and *M. guirali* based on MVZ 75748 and 81462, respectively). The sulcus spermaticus is centrolineal in *Pseudoxyrhopus*, *Heteroliodon*, and *Liophidium*, but the orientation is unknown in *Exallodontophis* and *Pararhadinaea*. Some species of the African genera have unusual structures, such as the trilobed apical morphology of *Lycophidion variegatum* (Branch, 1976) and large nude basal pockets in *Mehelya* (personal observations). Hemipenes of *Mehelya* have extremely long, narrow lobes unlike *Pseudoxyrhopus* (Bogert, 1940; Doucet, 1963; personal observations) but reminiscent of some species of *Liophidium* (Domergue, 1983). No clearly derived hemipenial structures are known to be shared by *Lycophidion* or *Mehelya* and any Malagasy colubrids.

Until more comprehensive phylogenetic analyses including these genera have been completed it will not be possible to evaluate the extent to which the unusual dentition and jaw characters shared by these

African and Malagasy snakes are due to common ancestry, or are convergent specializations related to similar diets. The complexity of the colubrid radiation in Africa (Cadle, 1994) and the questionable monophyly of the clade of African hinged-toothed snakes (Bogert's Group II) makes these analyses exceedingly complex.

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SPECIMENS OF THE *PSEUDOXYPHOPUS* GROUP EXAMINED

Museum abbreviations are as follows.

AMNH	American Museum of Natural History, New York
BMNH	The Natural History Museum, London
CM	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts
MVZ	Museum of Vertebrate Zoology, University of California, Berkeley

- MNHN Muséum National d'Histoire Naturelle, Paris
- SMF Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt
- SMNS Staatliches Museum für Naturkunde in Stuttgart
- UMMZ University of Michigan Museum of Zoology, Ann Arbor
- USNM National Museum of Natural History, Washington, D.C.
- Unless otherwise noted, localities for these specimens were given by Raxworthy and Nussbaum (1994) for *Exallodontophis*, *Heteroliodon*, and *Pseudoxyrhopus* and by Domergue (1983) for *Liophidium*. Observations on dentition were made on specimens denoted as follows: SK = dry skull (all teeth examined); MT = maxillary teeth examined; DT = dentary teeth examined.
- Exallodontophis albignaci*. MNHN 1982.1221 (MT) (holotype). UMMZ 203642 (MT) (Antsiranana Prov.: Sambava Fivondronana: Marojejy Reserve, Manan-tinina River, 350 m elevation).
- Heteroliodon occipitalis*. BMNH 1946. 1.12.28 (MT) (holotype), 1930.7.1.238 (MT).
- Liophidium apperti*. MNHN 1982.442 (MT) (holotype).
- Liophidium chabaudi*. MNHN 1978. 2789 (MT) (holotype), 1978.2788 (MT).
- Liophidium rhodogaster*. MCZ 180381 (MT), 180382 (MT), 181169 (MT), 181170 (MT), 181171 (SK), 181172 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Talatakeley, Ranomafana National Park, approximately 950–1,000 m elevation).
- Liophidium therezieni*. MNHN 1982. 444 (MT) (holotype), 1978.1425 (MT).
- Liophidium torquatum*. BMNH 1946. 1.1.38 (MT) ("Madagascar;" holotype), 89. 4.11.10 ([Toamasina Prov.]: Antongil Bay). MCZ 181303 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: 6 km (by Route 25) W. Andranomaitso between Ifanadiana and Kianjavato, approximately 500–600 m elevation). MCZ 181305 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Ranomafana town, approximately 600 m elevation).
- Liophidium trilineatum*. BMNH 1946. 1.15.66 (MT) (holotype) ([Toliara Prov.]: Southwestern Madagascar).
- Liophidium vailanti*. MNHN 1901.186, 1901.187 (MT) (syntypes) ([Toliara Prov.]: Fort Dauphin and Isaka). MCZ 22203 (SK) (locality unknown).
- Pararhadinaea melanogaster*. SMF 17885 (old number 7313.1a) (MT, DT) (holotype [Antsiranana Prov.: Fivondronana Nosy Be]: Insel Nossibé). SMNS 4235 (MT, DT) (holotype of *Rhabdotophis subcaudalis* Werner, 1909. "Madagascar").
- Pararhadinaea melanogaster marojejyensis*. MNHN 1982.1220 (MT) (holotype [Antsiranana Prov.: Fivondronana Andapa]: "Forêt du massif montagneux du Marojejy" [Domergue, 1984]), here interpreted to be imprecise based on information provided by Charles P. Blanc. According to Blanc, the specimen was collected 19 December 1972 in pristine lowland rainforest on the coast.
- Pseudoxyrhopus ambreensis*. UMMZ 200061 (MT, DT), 200062 (MT), 200063 (MT), 203643, 203644.
- Pseudoxyrhopus inerinae*. BMNH 95.10.29.60 (MT, DT).
- Pseudoxyrhopus kely*. UMMZ 192022 (MT, DT).
- Pseudoxyrhopus microps*. CM 119068 (MT, DT).
- Pseudoxyrhopus quinquelineatus*. BMNH 93.9.6.2 (SK), 1930.7.1.236 (MT), 1930.7. 1.237 (MT, DT). USNM 149903 (MT, DT) ([Toamasina Prov.]: Perinet). MCZ 11651 (SK) ([Toamasina Prov.]: Swamp near Didy).
- Pseudoxyrhopus sokosoko*. UMMZ 203660, 203661 (MT), 209689 (MT).
- Pseudoxyrhopus tritaeniatius*. AMNH 60712 (MT, DT) (specific locality unknown). MNHN 1891.24 (MT) (holotype [probably Fianarantsoa Prov.]: "Betsileo"), 1898.7 (MT) (specific locality unknown). MCZ 180300 (Fianarantsoa Prov.: Fivondronana Ifanadiana: Route 25 between Ambatolahy and Ranomafana town),

182468 (SK) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Ranomafana National Park, mountain ridge N of Miaranony approximately 9.8 km [airline] WNW Tsarananana, Faravory River, approximately 1,100 m elevation), 182480 (MT) (Fianarantsoa Prov.: Fivondronana Ifanadiana: Talatakely, Ranomafana National Park, 970 m elevation).

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